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Seasonal Activity of *Ixodes dammini* in Relation to Lyme Disease-Infected White-Footed Mice, *Peromyscus leucopus*

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SEASONAL ACTIVITY OF *IXODES DAMMINI* IN RELATION TO LYME DISEASE-INFECTED WHITE-FOOTED MICE, *PEROMYSCUS LEUCOPUS*

BY

ZUHAIR S. AMR

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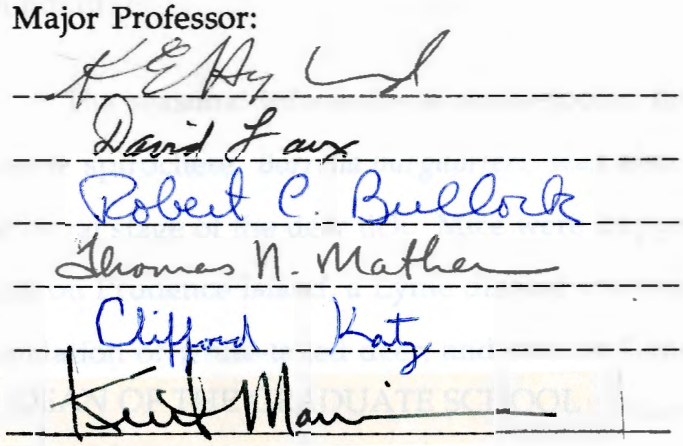

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ABSTRACT

This study evaluates the seasonal infestation rates of white-footed mice, *Peromyscus leucopus*, harboring immature stages of the deer tick, *Ixodes dammini*, at three sites on Prudence Island, Rhode Island, USA, a Lyme disease endemic area. Larval infestation rates varied from 46.0 larvae per mouse in August to none at all sites during November, while nymphal infestations ranged from 11.0 per mouse in June to none at all three sites in September through November. At all three study sites, the white-footed mouse appeared to be the most common host species in the wooded areas where larvae and nymphs of *I. dammini* are also abundant.

The seasonal infectivity of white-footed mice with the Lyme disease spirochete, *Borrelia burgdorferi*, was also monitored using the larval stage of the deer tick. Mice were trapped at four sites: three on Prudence Island, a Lyme disease endemic area with a large population of white-tailed deer; and one on Conanicut Island (Jamestown) with no white-tailed deer. All mice taken from Prudence Island were infective to laboratory-reared larvae with the highest infectivity from May to August. Larvae that fed on juvenile mice collected in September, October, and November were not infective. Mice originating from Conanicut Island were also not infective. This suggests, at least at these study sites, that the

presence of host-seeking *I. dammini* is a prerequisite to perpetuating spirochetes in white-footed mice. Furthermore, this study demonstrates that mice are infective to larval ticks during the peak larval season which extends from July to late October. It is presumed that these infected larvae would become infected nymphal ticks which emerge the following season.

Risk of Lyme disease transmission can be expressed as an Entomological Risk Index (ERI), a term that describes the relative abundance of infected deer tick nymphs per unit time. Variations in ERI were observed among the three sites and it was also found to change seasonally. The peak in ERI coincided with peak density of nymphal *I. dammini* and corresponded with the reported occurrence of Lyme disease in humans.

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PREFACE

This thesis is an integration of three separate studies. The first study addresses the risk of Lyme disease transmission in an endemic area during the months of the year when nymphal ticks are abundant. Transmission risk is expressed as an "Entomological Risk Index," describing the abundance of infected vector ticks in a local geographic area at a particular time of the year. The second study deals with the seasonal infestation of the white-footed mouse, *Peromyscus leucopus*, with the immature stages of the deer tick. This mouse is the principal host for *I. dammini* subadults. Moreover, it is the most common rodent in Lyme disease endemic areas in the Northeast. The infestation of *P. leucopus* by ticks was monitored at three study sites on Prudence Island to determine the role of this host in the life cycle of the deer tick. Seasonal infectivity of field-captured white-footed mice to the larval of *I. dammini* is evaluated in the third study. *Peromyscus leucopus* is the major reservoir of Lyme disease in northeastern United States.

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LITERATURE REVIEW

I. The Disease

Lyme disease, also known as Lyme borreliosis, is a human affliction caused by the spirochete, *Borrelia burgdorferi*, and is transmitted by several species of ticks of the genus *Ixodes* (Burgdorfer et al., 1982; Spielman et al., 1985). This disease has a wide spectrum of pathological effects and may involve multiple organ systems (Duray and Steere, 1986). Early manifestations of Lyme disease may include the appearance of a characteristic circular rash, erythema chronicum migrans (ECM), an erythematus papule or macule that forms within four to 20 days after the initial bite of an infected tick (Steere et al., 1977b). Such a rash is reported in 50 to 70% of the Lyme disease cases (Jost et al., 1988). Histologically, ECM is an infiltration of lymphoplasmacytes around dermal vessels (Duray, 1987). About half of the Lyme disease patients who developed this rash may show smaller multiple annular secondary lesions at different sites on the skin. If the patient remains untreated, the rash will spontaneously disappear within a month (it may last for one day to 14 months). Malaise, fatigue, fever, chills, sore throat, headache and generalized achiness are some of the other associated early symptoms (Steere et al., 1977a; Jost et al., 1988; Sigal, 1988).

A few months after the initial rash, 10 to 15% of patients may experience neurologic manifestations (Stiernstedt et al., 1986). Unilateral blindness caused by Lyme disease has been identified (Steere et al., 1985) where spirochetes were recovered from vitreous debris of one patient. Unilateral or bilateral facial paralysis may occur in up to 11% of patients (Clark et al., 1985), and bilateral keratitis and optic neuropathy are also seen

among Lyme disease patients (Baum et al., 1988; Schechter, 1986). Patients without the characteristic ECM may develop aseptic meningitis, encephalitis, cranial neuritis, motor and sensory radiculitis and myelitis of various combinations (Reik et al., 1979). One acute case of meningoencephalitis accompanied by slurred speech, seizure, hemiparesis and cerpospinal fluid pleocytosis due to Lyme disease was described by Feder et al. (1988). Moreover, *B. burgdorferi* organisms were seen in a brain autopsy of an Alzheimer's disease patient (MacDonald and Miranda, 1987). Finkel (1988) presented an extensive review on the neurologic manifestations of Lyme disease.

About 60% of Lyme disease patients develop arthritis. The initial signs usually appear within a few weeks to two years after onset of the disease (Steere et al., 1977a; 1979; 1980a). Disabling arthritis and erosive joint disease were reported by McLaughlin et al. (1986). Cardiac involvement may occur in about 10% of patients, usually two to three months after the appearance of the skin rash. Reversible and fatal myocarditis have been reported (Marcus et al., 1985). Additionally, mild congestive heart failure and multi-focal damage proximal to the bundle of His and ventricular condition system were described among Lyme disease victims (Steere et al., 1980b). Other clinical observations associated Lyme disease with atrioventricular block, myopericarditis and left ventricular dysfunction (Olson et al., 1986). Acute necrotizing splenitis, with extensive necrosis and inflammation of the spleen and a massive number of *Borrelia* organisms, was observed in a Lyme disease patient by Rank et al. (1989).

A. Historical Background.

Erythema migrans, a migratory annular skin rash following a tick bite by the sheep tick, *Ixodes ricinus*, was originally described in Sweden by Afzelius (1910). Subsequently, this syndrome was refereed to as "Erythema Chronicum Migrans". Later, Lipschutz (1913) suggested that this skin illness is caused by bacteria transmitted by ticks. Gelbjerg-Hansen (1945) suggested that ECM was an allergic reaction in certain individuals. Hellestrom (1951) reported ECM cases following tick bites and made reference to a positive response of these patients to penicillin treatment. The first evidence that ECM is caused by an infectious agent that responded to penicillin treatment was given by Binder et al. (1955). He transplanted pieces of skin from patients with the rash to healthy individuals, who later developed the characteristic rash. Lennhoff (1951) referred to spirochetal elements in skin rashes obtained from ECM patients, but it was over 30 years later that Burgdorfer et al. (1982) finally confirmed that a spirochete was the etiologic agent for this disease.

The first human case of ECM in the United States was reported from Wisconsin (Scrimenti, 1970). In 1975, Allen Steere and his associates observed "juvenile rheumatoid arthritis" following an outbreak in southwestern Connecticut and it was referred to as "Lyme disease" or "Lyme arthritis" (Steere et al., 1977b). Although the etiologic agent was not known, Steere and Malawista (1979) correlated the geographical distribution of the disease with the natural distribution of the newly described deer tick, *Ixodes dammini*. Yale University scientists studied many viruses, rickettsiae and piroplasms to demonstrate serological relationships with serum obtained

from Lyme disease patients and also examined *I. dammini* for the presence of viral agents.

In 1982, Burgdorfer and his colleagues observed poorly stained spirochetes obtained from the intestinal tract of the deer tick, *I. dammini*, collected from Long Island, New York (Burgdorfer et al., 1982). Further studies demonstrated the presence of similar spirochetes in both nymphal and adult stages of the deer tick (Bosler et al., 1983). Meanwhile in Europe, spirochetes were seen in the sheep tick, *I. ricinus* (Burgdorfer et al., 1983). Barbour et al. (1983) demonstrated the irrefutable evidence that these spirochetes reacted immunologically with sera obtained from Lyme disease patients and that this malady is caused by tick-borne spirochetes. Subsequently, the etiologic agent was described and named *Borrelia burgdorferi* in recognition of its discoverer, Dr. Willy Burgdorfer of the Rocky Mountain Laboratory in Hamilton, Montana (Johnson et al., 1984). In subsequent years much efforts has been undertaken at several institutions to understand the epidemiology of Lyme disease, including the enzootic interaction of wild animals and other arthropods.

B. Global Distribution of Lyme Disease.

Lyme borreliosis has been reported from many northeastern states including Massachusetts (Lastavica et al., 1989), Connecticut, Rhode Island (Brondum et al., 1988), New York (Hanrahan et al., 1984; Benach and Coleman, 1986; Williams et al., 1986) and New Jersey (Ward, 1981; Bowen et al., 1984). It has also been found in the West (California, Oregon, Nevada and Utah) and in the Midwest including Minnesota (Osterholm et al., 1984) and Wisconsin (Dryer et al., 1979; Davis et al., 1984) . Currently, the disease is known from 43 states (Ciesielski et al., 1988; Tsai et al., 1989). It seems that

this illness exhibits a geographic progression and new foci are formed in areas where the disease was not previously known (Lastavica et al., 1989, Schulze et al., 1986b)

Indigenous cases of Lyme disease have been diagnosed in Canada (Doby et al., 1986; Lycka, 1986). In Europe, this illness was reported from Belgium (Huaux et al., 1987; Huaux et al., 1988), Ireland (Doby et al., 1988b), the Soviet Union (Korenberg et al., 1986; Deknenko et al., 1988), Czechoslovakia (Kmety et al., 1986), Germany (Caflisch et al., 1984; Herzer et al., 1986; Munchhoff et al., 1986; Paul et al., 1986; Schmidt et al., 1986; Schonberg et al., 1988), Austria (Stanek et al., 1986; Schumutzhard et al., 1988), Finland (Kovanen et al., 1986), France (Doby and Couatarmanac'h, 1986; Dournon and Assous, 1986), Italy (Fumarola et al., 1986; Trevisan et al., 1986), Sweden (Hovmark et al., 1988; Stiernstedt, 1985), Switzerland (Aeschlimann et al., 1986), Hungary (Bozsik et al., 1986) and Denmark (Hansen et al., 1986). In the Far East, Lyme disease was described from Japan (Kawabata et al., 1987) and China (Ai et al., 1988). Moreover, local human cases were reported from Australia (Stewart et al., 1982).

C. Some Epidemiological Aspects of Lyme Disease.

The risk of acquiring Lyme disease is correlated with the distribution of *I. dammini* (Steere and Malawista, 1979). Most Lyme disease cases are attributed to bites by nymphal stage ticks. Because of their small size, feeding ticks may go unnoticed for several days. These ticks are abundant during the early summer season when people tend to participate in outdoor activities. *Ixodes dammini* nymphs feed principally on white-footed mice, *Peromyscus leucopus*, which are important reservoir hosts for *B. burgdorferi*.

Seasonal transmission of Lyme disease has been positively correlated with the seasonal activity of the nymphal stage of the deer tick. Piesman et al. (1987) showed that Lyme disease transmission is highest during May and June. Moreover, Falco and Fish (1988a) demonstrated the presence of *I. dammini* ticks in the vicinity of Lyme disease patient's houses. They concluded that infection may be acquired near the home as well as in wooded areas infested with ticks.

Leisure activities, including hiking, camping, hunting, and field-related occupations (military trainees, forestry rangers, landscapers, naturalists and wood cutters) may result in higher exposure to infected nymphs in woodlands. In Europe, Paul et al. (1986) indicated that 12.8% of *Ixodes ricinus* ticks collected by tick-bite victims harbored *B. burgdorferi* and that the Lyme disease manifestation rate was 4%. Similarly, Costello et al. (1989) reported an infection icidence of 3% among patients from Connecticut who reported having attached *I. dammini*. Of these ticks, six out of 29 were found infected with *B. burgdorferi*. Schmutzhard et al. (1988) conducted a prospective study on infection with Lyme disease following tick bites among military recruits in Austria. Of 50 individuals bitten by ticks, two showed primary symptoms (ECM) and 11 had a significant increase in serum titer against *B. burgdorferi*. In another study of 126 tick bite cases, 76.2% were bitten by the different stages of the deer tick but only two patients developed clinical manifestation of Lyme disease (Falco and Fish, 1988b).

Various approaches have been suggested to quantify the risk of Lyme disease transmission. Falco and Fish (1989b) described "Encounter distance" to determine the relative risk of Lyme disease transmission. It is defined as

the mean number of meters traveled before encountering a nymphal or adult deer tick. Falco and Fish (1989a) also recommended using carbon dioxide baited tick traps to determine the human risk for Lyme disease. Lane and Regner (1989) proposed the use of the brush rabbit, *Sylvilagus bachmani* (Waterhouse), and the black-tailed rabbit, *Lepus californicus* Gray, as sentinels for Lyme disease surveillance. They showed that 90% of both sentinels revealed a significant titer against *B. burgdorferi.*

D. Etiologic Agent of Lyme Disease.

Spirochetes are helically-shaped bacterial organisms with a characteristic anatomy and pattern of locomotion. They belong to the order Spirochaetales, which consists of two families comprising five genera. The genera, *Borrelia* and *Treponema*, contain spirochetes that are pathogenic to man and animals. Morphologically, they have a multilayered outer envelope that surrounds the protoplasmic cylinder, which consists of a peptidoglycan layer, cytoplasmic membrane and the enclosed cytoplasmic contents. Axial filaments and axial fibrils (periplasmic flagella) occur between the outer envelope and the protoplasmic cylinder (Johnson et al., 1984; Barbour and Hayes, 1986).

Evolutionarily, some workers believe that *Borrelia* developed primarily as a parasite of ticks and that mammals are accidental hosts (Felsenfield, 1971) while Hoogstraal (1979) claimed that *Borrelia* developed as a symbiont of ticks but acts as a parasite of mammals.

The Lyme disease spirochete, *Borrelia burgdorferi* Johnson et al., 1984, was described from an isolate originating from an adult *I. dammini* tick collected on Shelter Island, New York. This spirochete is helical with a

diameter of 0.18 to 0.25 and a length of 2 to 30 μm (Fig. 1). An average of seven periplasmic flagella are positioned at each end of the organism and overlap around the central area of the cell. *Borrelia burgdorferi* is gram negative, with optimal growth temperature of 34^0 C to 37^0 C and a generation time of 11 to 12 hours at 35^0 C (Barbour, 1984).

Transovarial transmission of *B. burgdorferi* in *I. dammini* was studied by Piesman et al. (1986) and Magnarelli et al. (1987). Both studies indicated that this phenomenon seems to be insignificant in disease transmission and may be of a limited importance in maintaining *B. burgdorferi* in nature. Of 2297 larval *I. dammini* examined for the presence of *B. burgdorferi*, 44 were positive with an overall rate of 1.9% (Magnarelli et al., 1987). Similarly, Piesman et al. (1986) detected spirochetes in 0.7% of field collected larvae. However, Burgdorfer et al. (1983) reported transovarial infection of 100% and 60% of the larval progeny of two *Ixodes ricinus* females that had fed on *B. burgdorferi*-infected white rabbits. Likewise, Lane and Burgdorfer (1987) showed that one of three field-collected *I. pacificus* females with spirochetes produced 100% infected progeny that also maintained the spirochetes transstadially.

Burgdorfer et al. (1988) investigated the development of *B. burgdorferi* in *I. dammini*. They found spirochetes in the midgut region in the majority of infected ticks, and spirochetes sometimes penetrating the gut wall, causing systemic infection in the central ganglia, ovary and malpighian tubules. Moreover, they discovered that the longer the interval between engorgement and dissection, the greater the number of ticks demonstrating generalized infection.

Borrelia burgdorferi have been isolated from a number of birds and wild mammals. White-footed mice are the primary animals harboring the spirochete (Anderson and Magnarelli, 1983; Bosler et al., 1983; Anderson and Magnarelli, 1984; Levine et al., 1985; Loken et al., 1985; Anderson et al., 1986b; Anderson et al., 1987a; Anderson et al., 1987b; Godsey et al., 1987), but it has also been found in meadow voles (Bosler et al., 1983; Anderson et al., 1986b; Anderson et al., 1987a), the woodland jumping mouse (Anderson and Magnarelli, 1984), the eastern chipmunk (Anderson et al., 1985), raccoons and white-tailed deer (Anderson et al., 1983; Bosler et al., 1983; Bosler et al., 1984). *Borrelia burgdorferi* was isolated and cultured from three species of birds, a veery, a rose-breasted grosbeak and a yellow-throat (Anderson et al., 1986a).

Several domestic animals are affected by *B. burgdorferi* infection. Dogs were found to be at higher risk for infection than humans (Eng et al., 1988). In Wisconsin, 53% of 380 dogs examined showed a significant titer for *B. burgdorferi* (Burgess, 1986) and similar results were obtained in France (Doby et al., 1988a). Schulze et al. (1986a) reported an infection rate of 34.7% with the spirochete among dogs from seven municipalities in New Jersey. They recommended the use of dog serosurveys for epidemiological surveillance for Lyme disease. Clinically, dogs develop arthritis similar to that seen in humans (Lissman et al., 1984; Kornblatt et al., 1985).

Burgess and Mattison (1987) suggested an association with encephalitis in a horse heavily infected with *B. burgdorferi*. Lindenmeyer et al. (1989) indicated significant variation in Lyme disease infection rates among horses in two counties in Massachusetts where Lyme disease is prevalent. Horses

and cows are reported to show lameness, swollen joints and arthritis (Burgess, 1988; Cohen et al., 1988).

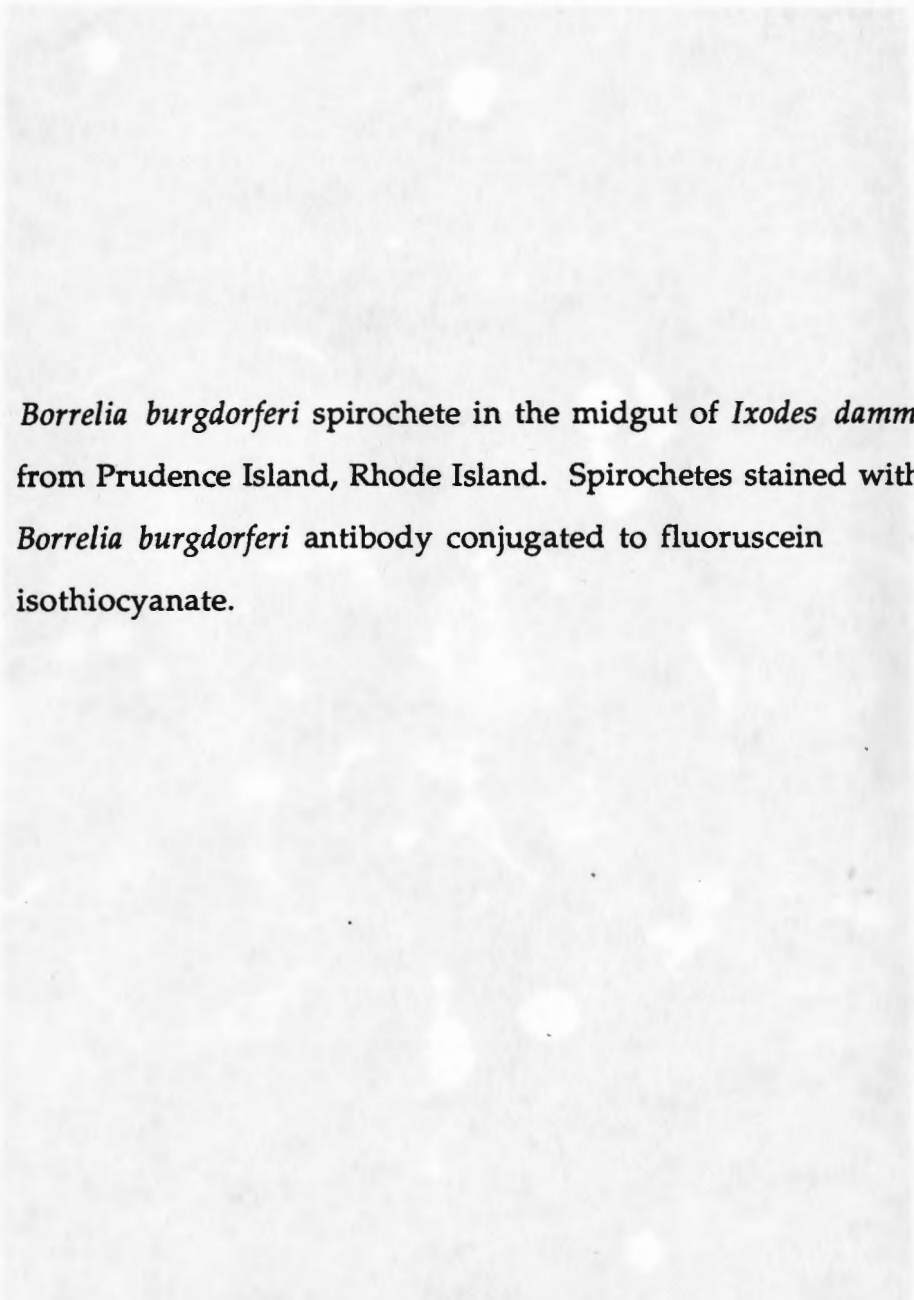
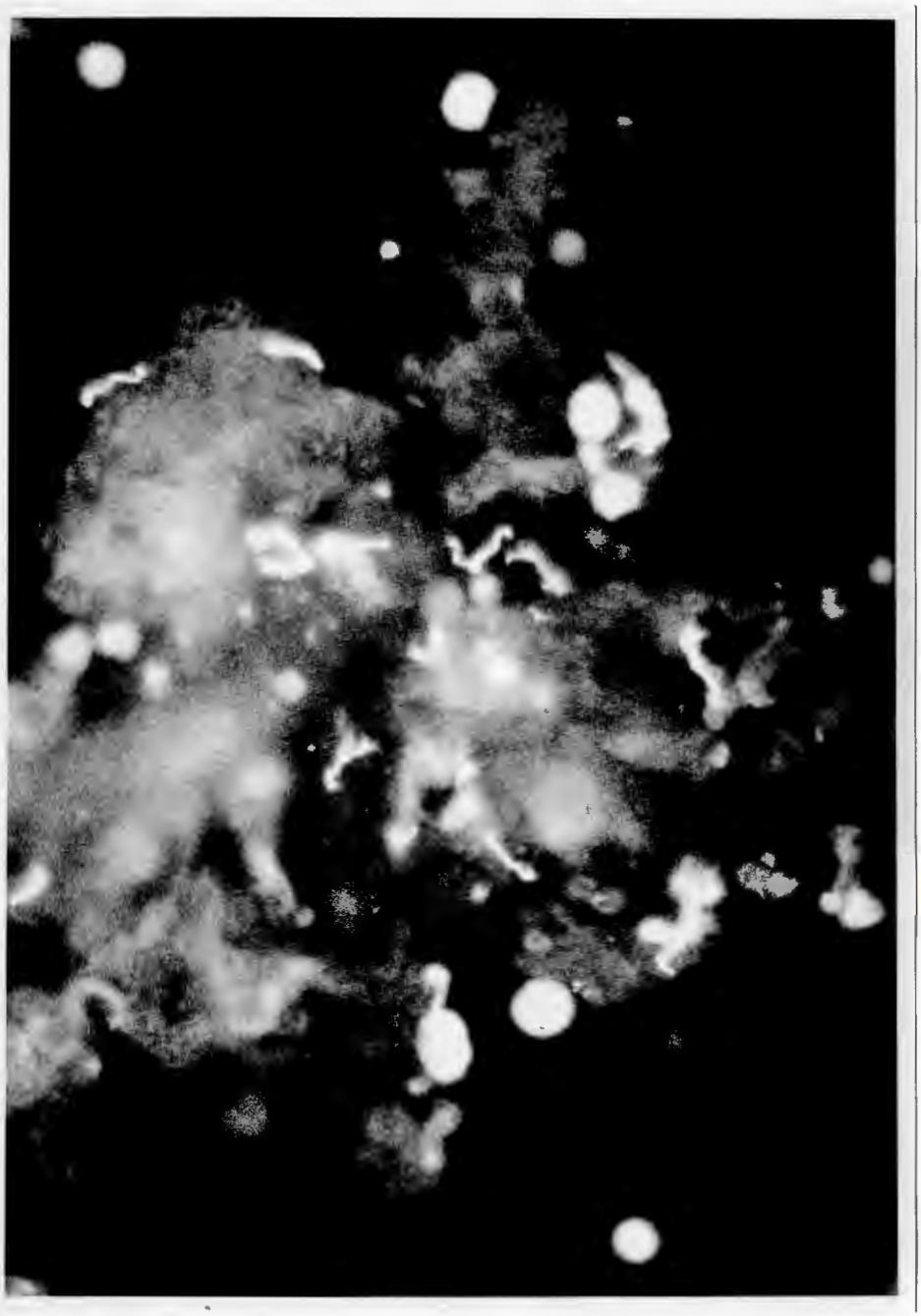


Fig. 1. *Borrelia burgdorferi* spirochete in the midgut of *Ixodes dammini* from Prudence Island, Rhode Island. Spirochetes stained with anti-*Borrelia burgdorferi* antibody conjugated to fluoruscein isothiocyanate.



II. Transmission of Lyme Disease Spirochetes

A. The Tick Vector, *Ixodes dammini*.

The genus *Ixodes* includes about 250 species worldwide, of which 35 are known to occur in North America (Keirans and Clifford, 1978). Ticks belonging to this genus are characterized by the absence of festoons, and the presence of an anal groove (Cooley and Kohls, 1945; Clifford et al., 1961). *Ixodes dammini* Spielman et al., 1979, was erected to replace the name known as *Ixodes scapularis* in the Northeast. Recently, Keirans and Litwak (1989) differentiated *I. dammini* and *I. scapularis* in a pictorial key for adult ixodid ticks east of the Mississippi River. Spielman et al. (1979) observed the resemblance of these two forms, but noticed certain structural differences, particularly in the nymph. They concluded that the New England population represented a new species (Fig. 2).

Spielman et al. (1985) presented a chronological review of the distribution of *I. dammini* in the United States. This species occurs in Maine, coastal Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Delaware, Pennsylvania and Virginia. It has also been reported in Wisconsin and Minnesota. Scarcity of specimens in museums has lead to the belief that *I. dammini* is expanding its range and increasing in density. This statement is at least true in Rhode Island, where this tick was formerly rare, but specimens have been collected recently from wild animals or obtained from people who were bitten by immature or adult stages of the deer tick (Hyland, unpublished).

Fig. 2. The nymphal stage of the deer tick, *Ixodes dammini*.

Ginsberg and Ewing (1989b) studied *I. dammini* in different habitats on Fire Island, New York. They found that questing nymphs and larvae were very abundant in wooded areas, especially in leaf litter, rather than open grass-land habitats. However, the number of immatures parasitizing the white-footed mice was not significantly different among various types of habitats. Adult ticks were more common on high shrubs (about one meter above ground level) rather than in grassy or low shrub habitats. Similar habitat is found on Prudence Island (Figure 3). The distribution of immature ticks may be due to the microclimatic conditions that the ticks experience or it may be due to the habitat preference of their hosts, particularly white-footed mice. Because adult *I. dammini* females feed principally on white-tailed deer, questing higher on vegetation may be an adaptation related to host-seeking success.

The distribution of *Ixodes dammini* follows that of the white-tailed deer (Piesman and Spielman, 1979; Spielman et al., 1979; Anderson and Magnarelli, 1980; Spielman et al., 1985). Ealier in the century when the deer population was low, this tick species likely had a limited distribution. However, the enormous increase in white-tailed deer populations in recent years has allowed the tick to expand its range along the coastal regions of the east coast (Spielman et al., 1985). Wilson et al. (1985) observed that larval ticks were abundant on islands inhabited by deer and absent or scarce on islands lacking deer. They also noted a decline in immature ticks infesting mice a year after removal of deer, however questing adults were abundant for four winters after being denied the deer hosts (Wilson et al., 1988).

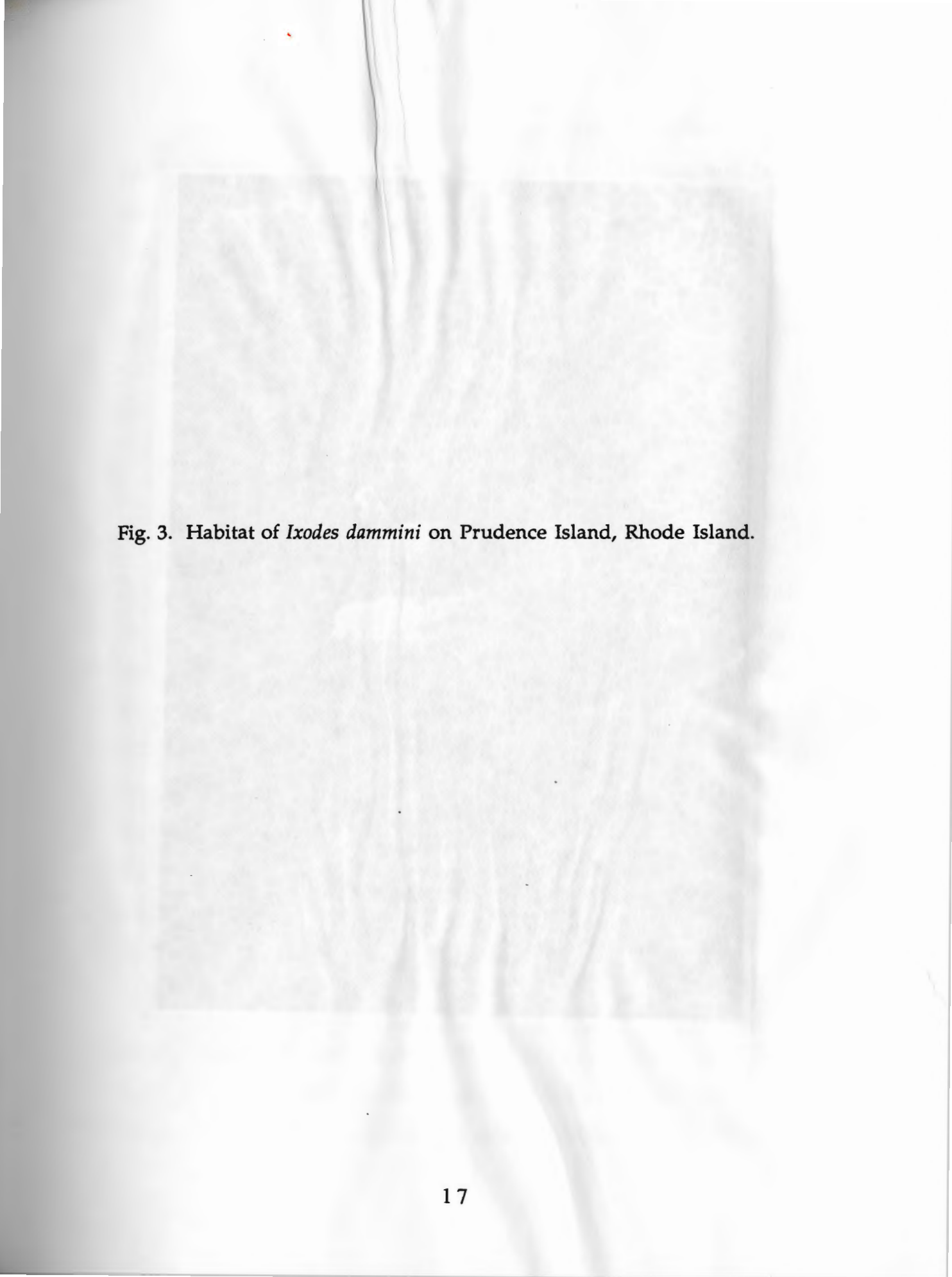


Fig. 3. Habitat of *Ixodes dammini* on Prudence Island, Rhode Island.

Schulze et al. (1984b) investigated the effect of climatic factors on the spatial distribution of *I. dammini* in New Jersey. They stated that rainfall and temperature have little impact on the distribution of the deer tick, and they concluded that physiogeographic regions are the key element determining the spatial distribution of the tick. This conclusion was based upon habitat and physiographic similarities of Lyme disease endemic regions throughout the Northeast. Moreover, they questioned the distance-elevation theory (Carey et al., 1980) that was proposed to be the major limiting factor for *I. dammini* distribution

Ixodes dammini is a three-host tick that requires two or more years to complete its life cycle (Fig. 4). This tick species takes three blood meals throughout its life cycle, one during each stage. The life cycle commences when the engorged overwintering female deposits its eggs in the spring (McEnroe, 1984; Spielman et al., 1985). These eggs hatch into the six-legged larval stage, which generally find either a small mammal or bird for its first blood meal. Although larvae are found on mice from May to July, they are particularly abundant during August, and virtually non-existed by November. Spielman (personal communication) suggested that larvae found in May and June are the winter survivors of the previous summer season, and that August larvae hatch from eggs produced by the fall or spring-engorged females.

After feeding to repletion, larvae drop from the host on soil and leaf litter or inside the rodent burrows. They molt into the eight-legged nymphal stage in the spring of the ensuing year. Nymphs will feed to repletion upon a variety of hosts, including humans, in three to four days, after which they

detach, dropping to the ground, where they will transform into the adult. Adults are active during the fall and throughout winter until the following spring. Foxes, raccoons, dogs and humans are acceptable hosts, however, the white-tailed deer is the preferred host for the female tick. Males are not known to feed on blood, but are found mating with feeding females (Spielman et al., 1985).

The deer tick has a broad range of mammalian and avian hosts (Spielman et al., 1979; Main et al., 1982; Anderson and Magnarelli, 1984; Schulze et al., 1986b; Battaly et al., 1987; Anderson, 1988; Fish and Dowler, 1989; Wiesbrod and Johnson, 1989). Usually, the immature stages feed on small- medium- and large-sized mammals and ground-feeding birds. Twenty-nine mammals belonging to seven orders and 54 bird species representing 14 families have been found infested with immature *I. dammini* (Tables 1 and 2). However, some species are more commonly utilized than others (Spielman et al., 1985). Several studies confirmed that the white-footed mouse is the preferred host for *I. dammini* subadults (Main et al., 1982; Levine et al., 1985; Mather et al., 1989b). Moreover, eastern chipmunks and gray squirrels were found to harbor a noticeable number of the immature stages (Main et al., 1982).

Adult *I. dammini* females are known to feed on medium and large sized mammals. They have been taken from opossums, woodchucks, gray squirrels, gray foxes, red foxes, stripped skunks, dogs, cats, black bears, horses, white-tailed deer and humans (Piesman and Spielman, 1979; Main et al., 1982; Anderson and Magnarelli, 1984; Godsey et al., 1987; Drew et al., 1988; Kazmierczak et al., 1988; Telford et al., 1988; Fish and Dowler, 1989).

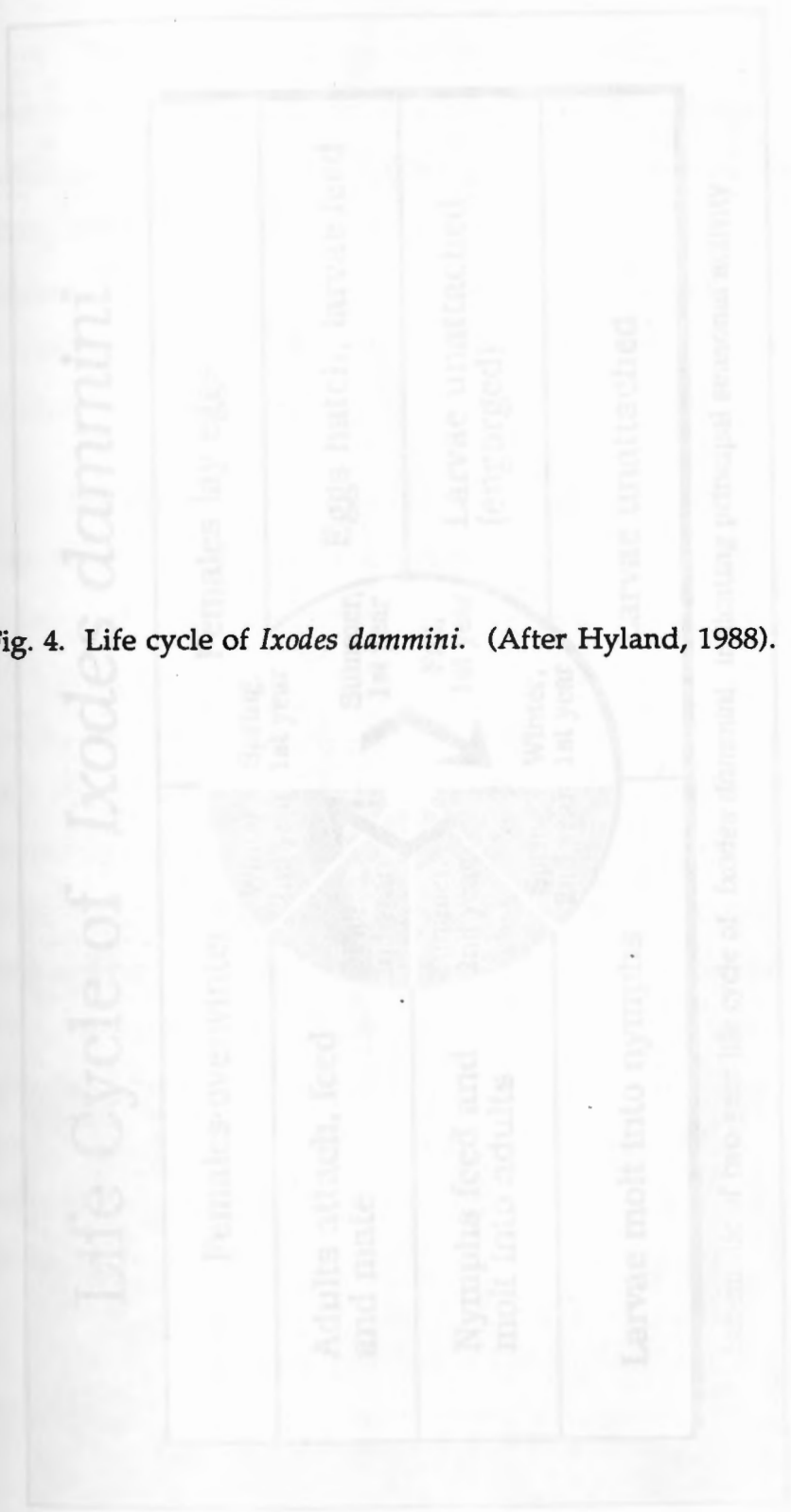
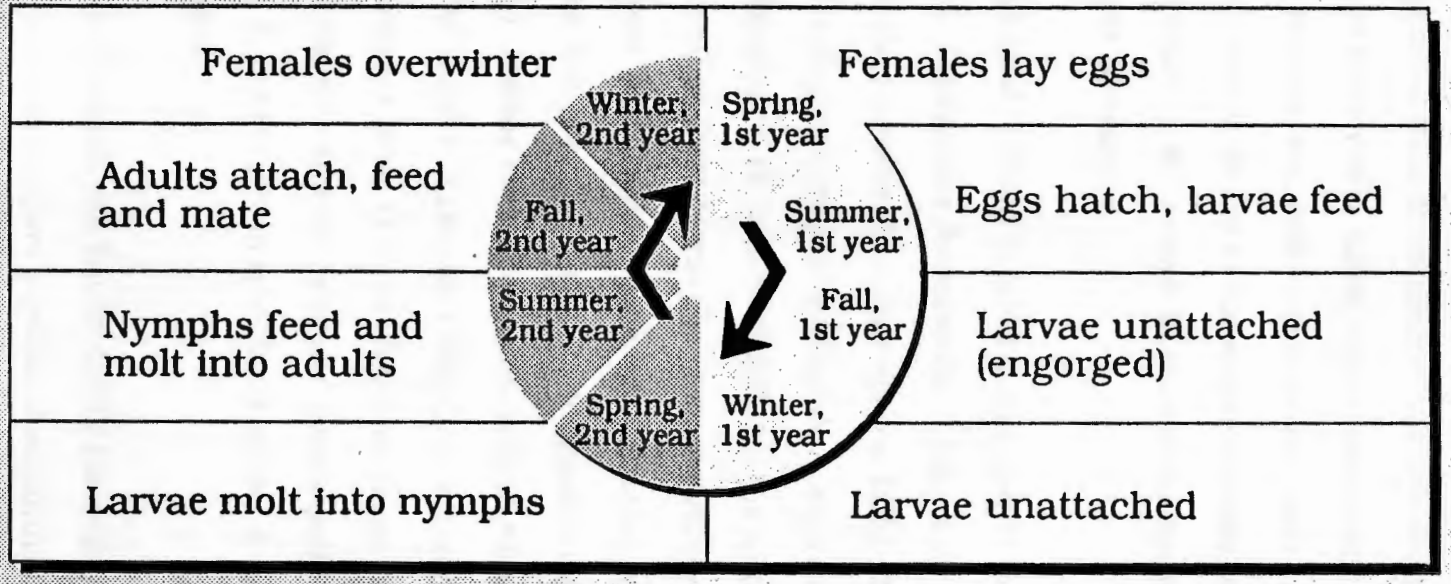


Fig. 4. Life cycle of *Ixodes dammini*. (After Hyland, 1988).

Life Cycle of *Ixodes dammini*



Schematic of two-year life cycle of *Ixodes dammini* indicating principal seasonal activity

B. Other Tick Vectors for Lyme Disease in North America.

Three species of the genus *Ixodes* in North America are implicated as vectors for Lyme disease transmission, namely: the western black-legged tick, *Ixodes pacificus* Cooley and Kohls, distributed along the west coast (Burgdorfer and Keirans, 1983), the southern black-legged tick, *Ixodes scapularis* Say, which occurs in the southern states, and the deer tick, *Ixodes dammini* Spielman et al., known in the northeastern states and in Wisconsin and Minnesota.

Schulze et al. (1984a) isolated *B. burgdorferi* from specimens of the lone star tick, *Amblyomma americanum* (Linnaeus), recovered from patients with the characteristic Lyme disease ECM. They also found that 9.1% of field collected nymphal and adult *A. americanum* carried the spirochete. Magnarelli et al. (1986a) detected the spirochete in 3.5% of 173 lone star ticks taken from North Carolina. Rawlings (1986) isolated *B. burgdorferi* from *Amblyomma* specimens collected from Texas. The spirochete has also been cultivated from American dog ticks, *Dermacentor variabilis* (Say), feeding on white-footed mice (Anderson et al., 1985; Anderson et al., 1987c). Rawlings (1986) has reported unidentified spirochetes isolated from *D. variabilis* from Texas. Moreover, *Rhipicephalus sanguineus* (Latreille) and *Dermacentor parumapertus* Neumann, were infected with *B. burgdorferi* in east Texas where *R. sanguineus* is common (Rawlings, 1986).

Recently, Piesman and Sinsky (1988) showed that larval *A. americanum* from Alabama are capable of acquiring *B. burgdorferi*, but they

Table 1
Avian Hosts for the Deer tick, *Ixodes dammini*

Common Name	Scientific Name	Stage		Reference
		Larva	Nymph	
Family Phasianidae				
Wild Turkey	*Meleagris gallopavo*		x	Anderson, 1988.
Northern Bobwhite	*Colinus virginianus*	x	x	Spielman et al., 1979.
Family Scolopacidae				
American Woodcock	*Scolopax minor*		x	Anderson, 1988.
Family Tyrannidae				
Eastern Phoebe	*Sayornis phoebe*	x		Main et al., 1982; Anderson & Magnarelli, 1984; Anderson et al., 1986.
Family Corvidae				
Blue Jay	*Cyanocitta cristata*	x	x	Main et al., 1982; Anderson & Magnarelli, 1984; Battaly et al., 1987.
Family Paridae				
Black-capped Chickedee	*Parus atricapillus*	x	x	Anderson & Magnarelli, 1984; Shulze et al., 1986; Battaly et al., 1987.
Tufted Titmouse	*Parus bicolor*		x	Main et al., 1982; Wiesbrod & Johnson, 1989.
Family Sittidae				
White-breasted Nuthatch	*Sitta carolinensis*	x	x	Anderson & Magnarelli, 1984; Anderson et al., 1986.
Family Certhiidae				
Brown Creeper	*Certhia americana*		x	Anderson, 1988.
Family Troglodytidae				
House Wren	*Troglodytes aedon*	x	x	Anderson & Magnarelli, 1984.
Carolina Wren	*Thryothorus ludovicianus*	x	x	Schulze et al., 1986.
Family Muscicapidae				
American Robin	*Turdus migratorius*	x	x	Spielman et al., 1979; Anderson & Magnarelli, 1984.
Swainson's Thrush	*Catharus ustulatus*	x	x	Anderson & Magnarelli, 1984.
Hermit Thrush	*Catharus guttatus*		x	Anderson & Magnarelli, 1984.
Veery	*Catharus fuscescens*		x	Anderson et al., 1986; Schulze et al., 1986; Weisbrod & Johnson, 1989.
Wood Thrush	*Hylocichla mustelina*	x	x	Main et al., 1982; Anderson et al., 1986; Schulze et al., 1986; Battaly et al., 1987.
Family Mimidae				
Gray Catbird	*Dumetella carolinensis*	x	x	Spielman et al., 1979; Anderson & Magnarelli, 1984; Shulze et al., 1986; Battaly et al., 1987; Mather et al., 1989; Weisbrod & Johnson, 1989.
Brown Thrasher	*Toxostoma rufum*		x	Spielman et al., 1979.

Table 1 (Continued)

Common Name	Scientific Name	Stage		Reference
		Larva	Nymph	
Family Sturnidae				
European Starling	*Sturnus vulgaris*		x	Anderson, 1988.
Family Vireonidae				
White-eyed Vireo	*Vireo griseus*	x	x	Anderson & Magnarelli, 1984; Anderson et al., 1986.
Red-eyed Vireo	*Vireo olivaceus*		x	Anderson, 1988.
Family Emberizidae				
Kentuckey Warbler	*Oporornis formosus*		x	Anderson, 1988.
Mourning Warbler	*Oporornis philadelphia*	x		Wiesbrod & Johnson, 1989.
Connecticut Warbler	*Oporornis agilis*	x		Wiesbrod & Johnson, 1989.
Wilson Warbler	*Wilsonia pusilla*		x	Wiesbrod &Johnson, 1989.
Canada Warbler	*Wilsonia canadensis*	x		Wiesbrod &Johnson, 1989.
Hooded Warbler	*Wilsonia critrina*		x	Anderson et al., 1986; Battaly et al., 1987.
Nashville Warbler	*Vermivora ruficapilla*	x	x	Wiesbrod &Johnson, 1989.
Blue-winged Warbler	*Vermivora pinus*	x	x	Anderson & Magnarelli, 1984; Anderson et al., 1986; Battaly et al., 1987.
Pine Warbler	*Dendroica pinus*	x		Anderson & Magnarelli, 1984.
Yellow-rumped Warbler	*Dendroica coronata*	x		Wiesbrod & Johnson, 1989.
Yellow Warbler	*Dendroica petechia*	x	x	Anderson et al., 1986;
PrairieWarbler	*Dendroica discolor*		x	Anderson, 1988.
Worm-eating Warbler	*Helmitheros vermivorus*	x	x	Anderson, 1988.
Northern Waterthrush	*Seiurus noveboracensis*	x		Anderson & Magnarelli, 1984; Shulze et al., 1986; Weisbrod & Johnson, 1989.
Louisiana Waterthrush	*Seiurus motocilla*		x	Anderson & Magnarelli, 1984; Anderson et al., 1986.
Ovenbird	*Seiurus aurocapillus*	x	x	Anderson et al., 1986; Wiesbrod &Johnson, 1989.
Chipping Sparrow	*Spizella passerina*	x	x	Anderson & Magnarelli, 1984; Battaly et al., 1987
Field Sparrow	*Spizella pusilla*			Anderson & Magnarelli, 1984
Swamp Sparrow	*Melospiza geogiana*	x	x	Anderson & Magnarelli, 1984; Anderson et al., 1986; Weisbrod & Johnson, 1989.
Song Sparrow	*Melospiza melodia*	x	x	Weisbrod & Johnson, 1989.
Common Yellowthroat	*Geothlypis trichas*	x	x	Anderson & Magnarelli, 1984; Anderson et al., 1986; Shulze et al., 1986; Weisbrod & Johnson, 1989.
White-throated Sparrow	*Zonotrichia albicollis*	x		Anderson & Magnarelli, 1984; Weisbrod & Johnson, 1989.
American Redstart	*Setophaga ruticilla*	x		Wiesbrod & Johnson, 1989.
Yellow-breasted Chat	*Icteria virens*	x		Anderson & Magnarelli, 1984.
Red-winged Blackbird	*Agelaius phoeniceus*	x	x	Anderson & Magnarelli, 1984.
Common Grackle	*Quiscalus quiscula*	x	x	Main et al., 1982; Anderson & Magnarelli, 1984; Shulze et al., 1986.
Brown-headed Cowbird	*Molothrus ater*	x	x	Spielman et al., 1979; Anderson & Magnarelli, 1984; Battaly et al., 1987.
Northern Cardinal	*Cardinalis cardinalis*	x	x	Anderson & Magnarelli, 1984; Anderson et al., 1986; Shulze et al., 1986.
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	x	x	Anderson & Magnarelli, 1984; Anderson et al., 1986; Shulze et al., 1986; Battaly et al., 1987.
Black and White Warbler	*Mniotilta varia*		x	Anderson, 1988.
Rufous-sided Towhee	*Pipilo erythrophthalmus*	x	x	Main et al., 1982; Anderson & Magnarelli, 1984; Battaly et al., 1987.
Family Fringillidae				
Purple Finch	*Carpodacus purpureus*		x	Anderson & Magnarelli, 1984.

Table 2
Mammalian Hosts for the Deer Tick, *Ixodes dammini*

Common Name	Scientific Name	Stage			Reference
		Larva	Nymph	Adult	
Order Marsupialia					
Virginia Opossum	*Didelphis virginiana*	x	x	x	Spielman et al., 1979; Main et al., 1980; Anderson et al., 1983; Godsey et al., 1987; Fish & Dowler, 1989.
Order Insetivora					
Short-tailed Shrew	*Blarina brevicauda*	x	x		Piesman & Spielman, 1979; Spielman et al., 1979; Main et al., 1982; Anderson & Magnarelli, 1984; Godsey et al., 1987.
Masked Shrew	*Sorex cinereus*	x	x		Main et al., 1982; Godsey et al., 1987.
Smoky Shrew	*Sorex fumeus*	x	x		Main et al., 1982.
Eastern Mole	*Scalopus aquaticus*	x			Main et al., 1982.
Order Lagomorpha					
Eastern Cottontail	*Sylvilagus floridanus*	x	x		Piesman & Spielman, 1979; Spielman et al., 1979; Main et al., Godsey et al., 1987.
Order Rodentia					
Eastern Chipmunk	*Tamias striatus*	x	x		Piesman & Spielman, 1979; Spielman et al., 1979; Main et al., 1982; Anderson et al., 1983; Godsey et al., 1987.
Woodchuck	*Marmota monax*	x	x	x	Main et al., 1982; Godsey et al., 1987; Fish & Dowler, 1989.
Southern Flying Squirrel	*Glaucomys volans*	x	x		Anderson, 1988.
Red Squirel	*Tamiasciurus hudsonicus*	x	x		Main et al., 1982; Anderson et al., 1983; Godsey et al., 1987.
Gray Squirrel	*Sciurus carolinensis*	x	x	x	Spielman et al., 1979; Main et al., 1982; Fish & Dowler, 1989.
White-footed Mouse	*Peromyscus leucopus*	x	x		Piesman & Spielman, 1979; Spielman et al., 1979; Main et al., 1982; Anderson et al., 1983; Anderson & Magnarelli, 1984; Godsey et al., 1987.
Deer Mouse	*Peromyscus maniculatus*	x	x		Godsey et al., 1987.
Gapper's Red-backed Mouse	*Clethrionomys gapperi*	x	x		Main et al., 1982; Godsey et al., 1987.
Meadow Vole	*Microtus pennsylvanicus*	x	x		Hyland & Mathewson, 1961; Piesman & Spielman, 1979; Spielman et al., 1979.
Pine Vole	*Microtus pinetorum*	x	x		Hyland & Mathewson, 1961; Anderson, 1988.
Beach Vole	*Microtus breweri*		x		Anderson, 1988.
Norway Rat	*Rattus norvegicus*	x	x		Hyland & Mathewson, 1961; Piesman & Spielman, 1979; Main et al., 1982.
Woodland Jumping Mouse	*Napaeozapus insignis*	x	x		Main et al., 1982.
Maedow Jumping Mouse	*Zapus hudsonius*	x	x		Main et al., 1982.

Table 2 (Continued)

Common Name	Scientific Name	Tick Stage			Reference
		Larva	Nymph	Adult	
Order Carnivora					
Raccoon	*Procyon lotor*	x	x	x	Spielman et al., 1979; Main et al., 1982; Anderson & Magnarelli, 1984.
Gray Fox	*Urocyon cinereoargenteus*	x	x	x	Hyland & Mathewson, 1961; Anderson, 1988; Fish & Dowler, 1989.
Red Fox	*Vulpes vulpes*	x	x	x	Anderson, 1988.
Striped Skunk	*Mephitis mephitis*	x	x	x	Spielman et al., 1979; Godsey et al., 1987.
Black Bear	*Euarctos americanus*			x	Anderson, 1988.
Dog	*Canis familiaris*		x	x	Piesman & Spielman, 1979; Spielman et al., 1979.
Cat	*Felis catus*	x	x	x	Anderson, 1988.
Order Artiodactyla					
White-tailed Deer	*Odocoileus virginianus*	x	x	x	Hyland & Mathewson, 1961; Piesman & Spielman, 1979; Spielman et al., 1979; Main et al., 1981; Telford et al., 1988.
Horse	*Equus caballus*			x	Spielman et al., 1979.
Order Primates					
Human	*Homo sapien*	x	x	x	Spielman et al., 1979; Piesman & Spielman, 1979; Falco & Fish, 1988.

do not maintain it transstadially. They also found that lone star ticks originating from Texas fail to acquire the Lyme disease spirochete.

C. Other Arthropod Vectors for Lyme Disease.

A number of hematophagus arthropods harbor *B. burgdorferi*. Spirochetes isolated from the cat flea, *Ctenocephalidis felis*, react positively with monoclonal antibody against *B. burgdorferi* (Rawlings, 1986). Additionally, the spirochete has been detected in the flea, *Orchopeas leucopus* (Anderson and Magnarelli, 1984). Four mosquito species (*Aedes canadensis* (Theobald), *Aedes stimulans* (Walker), *Aedes triseriatus* (Say) and *Aedes vexanx* (Meigen)), four deer fly species (*Chrysops callidu* Osten Sacken, *Chysops macquarti* Philip, *Chrysops univittatus* (Macquart) and *Chrysops vittatus* Wiedemann) and four horse fly species (*Hybomitra hinei* (Johnaon), *Hybomitra lasiophthalma* (Macquart), *Tabanus pumilus* Macquart and *Tabanus lineola* Fabricius) have been found infected with *B. burgdorferi* (Magnarelli et al., 1986b; Magnarelli and Anderson, 1988). Although the presence of Lyme disease spirochetes has been demonstrated in mosquitoes, it was shown experimentally that the spirochete survived for less than a week after infection. Furthermore, infected mosquitoes fed on spirochete-free hamsters failed to transmit the infectious agent (Magnarelli and Anderson, 1988).

D. The Role of the White-footed Mouse.

Although *I. dammini* has a broad range of hosts (Main et al., 1982; Anderson and Magnarelli, 1984; Anderson, 1988; Fish and Dowler, 1989), white-footed mice appear to be the principal hosts of the pre-adult forms (Levine et al., 1985; Mather et al., 1989b). Levine et al. (1985) evaluated the

role of the white-footed mouse as a reservoir host for the Lyme disease spirochete. Based on the relative abundance of this host and the fact that most immatures are attached to *P. leucopus*, they concluded that the white-footed mouse is the principal reservoir host for *B. burgdorferi*. *Borrelia burgdorferi* has been isolated from white-footed mice throughout the year (Anderson et al., 1986b). The infection rate ranged from 20% during March to 80% in May among mice captured from East Haddam, CT, while during December and June infection rates were 8.3% and 90%, respectively, in mice collected from Waterford, CT.

In Rhode Island, Anderson and Magnarelli (1983) reported an average of six larvae (SD ±1.2) of *I. dammini* per mouse from samples collected during September and November, 1982. Spirochetes were recovered from the blood of one of 20 trapped mice. However, nine of 22 mice were seropostive with *B. burgdorferi* antibodies. Anderson et al. (1987) examined *P. leucopus* specimens collected from Prudence Island during 1984-1985. They found an average of 3.3 nymphs and 13.0 larvae per mouse during the months of June and August, respectively. Moreover, 33 of 129 attached larvae and six of 20 nymphs recovered from the mice were infected with *B. burgdorferi*. Twenty-five serum samples obtained from white-footed mice collected from inland areas in Rhode Island plus Block Island, Conanicut and Prudence Islands revealed an infection rate of 20% when examined using enzyme-linked immunosorbent assay (ELISA) but first 12% when using an indirect fluorescent antibody assay (IFA) (Magnarelli et al., 1988). Of seven mice trapped from Prudence Island during November, 1984, six were found to harbor the spirochete (Anderson et al., 1986b).

The ability of a host animal to transmit infection effectively to a vector is termed "competence." However, even though an animal demonstrates competence, this term is insufficient to describe the potential for a species or population of hosts to serve as a zootic resource for an infection. The term "reservoir host" implies that the animal contributes in some way to the maintenance or perpetuation of the infection. Thus, white-footed mice are not only tick hosts, but are competent reservoirs for Lyme disease spirochetes (Mather et al., 1989b). Several other hosts parasitized by immature deer ticks including white-tailed deer (Telford et al., 1988), catbirds (Mather et al, 1989a), and raccoons (Mather, personal communication) appear incompetent to serve as reservoirs.

Many other species of small mammals including chipmunks, shrews and meadow voles may be competent in transmitting spirochetes to ticks, but demonstrate a low reservoir potential relative to white-footed mice (Mather et al., 1989b). It is because of this unique position in the dynamics of zoonotic Lyme disease spirochete transmission that mice are the focus of the present study.

INTRODUCTION

Lyme disease has become an important public health concern in many parts of the United States (Schmid et al., 1985; Piesman, 1987; Tsai et al., 1989). Moreover, it seems that this illness exhibits a geographic progression and new foci are formed in areas where the disease was not previously known (Schulze et al., 1986b; Lastavica et al., 1989). This malady is caused by the spirochete, *Borrelia burgdorferi*, which in the Northeast is transmitted by the deer tick, *Ixodes dammini* (Spielman et al., 1985). The disease is a complex, multisystem affliction with broad clinical manifestations including arthritis, cardiac and neurologic complications (Reik et al., 1979; Steere et al., 1980b; Clark et al., 1985; McLaughlin et al., 1986; Olson et al., 1986).

The risk of acquiring Lyme disease is correlated with the distribution of *I. dammini* (Steere and Malawista, 1979). The larvae are most abundant in July and August, and by October their numbers have declined. The nymph, the second stage, is common from May to late July. The adult stage, including males and females, is active during fall and through the ensuing spring (Spielman et al., 1985). Most human cases of Lyme disease are attributed to nymphal tick bites. This may be attributed to the small size of this tick, permitting them to go unnoticed for several days, and their abundance during the early summer season when people favor outdoor oriented activities. Seasonal transmission of Lyme disease has been positively correlated with the seasonal activity of the nymphal stage. Piesman et al. (1987) showed that Lyme disease transmission is highest during May and June. Moreover, Falco and Fish (1988a) demonstrated the presence of *I. dammini* in the vicinity of Lyme disease patients residences.

They concluded that infection may be acquired at home as well as in wooded areas infested with ticks. In Europe, Paul et al. (1986) found that 12.8% of *Ixodes ricinus* collected from tick-bite victims harbored *B. burgdorferi* and that 4% developed Lyme disease. Similarly, Costello et al. (1989) reported an infection rate of 3% among Connecticut patients bitten by *I. dammini*. Of 29 ticks, six were found infected with *B. burgdorferi*. Schmutzhard et al. (1988) conducted a study of Lyme disease infection following tick bites among military recruits in Austria. Of 50 individuals bitten by ticks, two showed primary symptoms and 11 had a significant increase in serum titer against *B. burgdorferi*. Munchhoff et al. (1986) reported that 13.7% of 496 forest workers examined from Bavaria showed significantly elevated antibody titer against *B. burgdorferi*. In a study of 126 individuals bitten by ticks in New York, 76.2% were bitten by the different stages of the deer tick. Children under 10 years of age constituted over half of the tick-bite victims. However, only two patients developed clinical manifestation of Lyme disease (Falco and Fish, 1988b).

Different techniques have been suggested to quantify the risk of Lyme disease transmission. Encounter distance, a term coined by Falco and Fish (1989a), was used to determine the relative risk of Lyme disease transmission. It is defined as the mean number of meters traveled by a person before encountering a nymphal or adult deer tick. Falco and Fish (1989b) recommended the use of carbon dioxide baited tick traps to determine population levels for calculating the human risk of acquiring Lyme disease. Lane and Regner (1989) proposed the use of the brush rabbit, *Sylvilagus bachmani*, and the black-tailed rabbit, *Lepus californicus*, as sentinels for

Lyme disease surveillance. They showed that 90% of both sentinels revealed a significant titer against *B. burgdorferi.*

Recently, Ginsberg and Ewing (1989a) compared four sampling methods (walking, flagging, trapping and mouse collecting) to determine tick abundance. They concluded that flagging rather than walking or CO_2 traps is the method of choice for sampling *I. dammini* subadults.

Entomological Risk Index (ERI), is a novel term introduced by Mather (personal communication), for use in determining the risk for the transmission of Lyme disease or other tick-borne diseases. Mathematically, ERI is the proportion of infected ticks multiplied by the number of ticks collected per sample (exposure) time. This index expresses the risk of encountering infected ticks in a particular time frame and in a defined area.

Although *I. dammini* has a broad host range (Main et al., 1982, Anderson and Magnarelli, 1984; Schulze et al., 1986a and 1986b; Anderson, 1988; Fish and Dowler, 1989), the white-footed mouse, *Peromyscus leucopus,* appears to be the principal host (Levine et al., 1985, Donahue et al., 1987) in areas where the deer tick is abundant (Main et al., 1982). Levine et al. (1985) evaluated the role of the white-footed mouse as a reservoir host for the Lyme disease spirochete. Based upon the relative abundance of this host and parasitism by *I. dammini,* they concluded that the white-footed mouse is the principal reservoir host for *B. burgdorferi.* Moreover, they reported the seasonality of subadult infestations and abundance of *I. dammini* on *P. leucopus* from Crane's Beach, Massachusetts. Here, the larval stage of the deer tick acquires the Lyme disease spirochete while feeding on an infected competent host. After repletion, the larva molts into the nymph the

following season and seeks a host for its second blood meal (Donahue et al., 1987).

Peromyscus leucopus is widely distributed throughout the eastern United States, from Missouri to North Carolina and northward to southern Canada (Hamilton and Whitaker, 1979). Fluctuations in population density varies from 38 mice/hectare to 6 mice/hectare within two years (Wolff, 1986). Populations of this species are not strictly regulated by food supply (Krohne et al., 1988), rather by behavioral territoriality of both sexes (Metzgar, 1971). Home range for males is 634 m^2 and 511 m^2 for females (Wolff, 1986).

It is evident that white-footed mice are competent reservoir hosts for Lyme disease spirochetes (Mather et al., 1989b). Larval *I. dammini* ticks recovered from deer inhabiting a Lyme disease endemic area showed an infection rate of 1% (Telford et al., 1988). Non-infected larval ticks which were allowed to feed on field-captured catbirds, did not become infected with *B. burgdorferi*, while 76% of larvae derived from white-footed mice trapped from the same area did (Mather et al., 1989a).

Although several studies have examined the association of *I. dammini* subadults and their vertebrate hosts (Main et al., 1982; Anderson and Magnarelli, 1983; Anderson and Magnarelli, 1984; Anderson, 1988), few have investigated the seasonal infestation of white-footed mice (Piesman and Spielman 1979; Levine et al., 1985).

Determining an animal's infectivity to feeding vectors, and not merely its susceptibility to infection, is critical to establishing its reservoir potential. In this context, reservoir potential defines the contribution made

by a species or population of animals towards infecting vector populations (Mather et al., 1989a), while infectivity, or reservoir competency, is a biologic property of a particular animal or species. It is generally agreed that white-footed mice (*P. leucopus*) serve as the principal reservoir for the Lyme disease spirochete, *B. burgdorferi* (Levine et al., 1985; Donahue et al., 1987; Mather et al., 1989a). As soon as three weeks after inoculation by tick-bite, this animal efficiently infects nearly all host-feeding *I. dammini*, the tick vector. Furthermore, infectivity in the laboratory may extend, albeit with lower efficiency, for several months (Donahue et al., 1987; Piesman, 1988). Of course, the reservoir potential of *P. leucopus* for the Lyme disease spirochete will be greatest where this mouse exhibits a uniformly high degree of infectivity that persists for the tick season, particularly through the peak late summer period of larval tick activity (Wilson et al., 1985; Amr et al., unpublished).

Even though mice are highly susceptible to infection with the Lyme disease spirochete (Donahue et al., 1985), and this infection appears to persist (Anderson et al., 1987a; Magnarelli et al., 1988), the infectivity of this animal to ticks may not be uniformly high nor complete. In previous studies, spirochetal infectivity of mice has varied considerably. From one location in Massachusetts, 46.3% of nymphal *I. dammini* derived from mouse-fed larvae were infected with *B. burgdorferi* (Mather et al., 1989a), while at a different location, mice infected 75.8% of all ticks feeding upon them (Mather et al., 1989b). However, in each of these studies the infectivity of just one population of mice was examined and for just one point in time. There are several factors that could affect an animal's infectivity. Age-related, geographic, or even individual variation in susceptibility might

influence spirochetal infectivity, as could temporal or seasonal factors. Furthermore, the level, or number of inoculations or the animal's immune status could also affect infectivity. Thus, before assuming that spirochetal infectivity exhibited by mice is constant, it seemed reasonable to evaluate concurrently the infectivity of several populations at various points in time. Therefore, we set out to assess both the seasonal and geographic variation in the spirochetal infectivity of white-footed mice.

The present study investigates the infection rate of *I. dammini* host-seeking nymphs with *B. burgdorferi* to : (1) determine the seasonal risk pattern of Lyme disease in an endemic area, (2) to examine and compare the seasonal infestation of immature stages of *I. dammini*, and 3) to determine the seasonal infectivity of white-footed mice to larval deer ticks with *B. burgdorferi*, in three sites on Prudence Island, Rhode Island, USA.

MATERIALS AND METHODS

The primary field sampling site selected for this study is Prudence Island, located in Narragansett Bay, Rhode Island, is 8 kilometers long, 0.8 kilometer wide and comprises approximately 1,528 hectares. About one-third of the island consists of several wildlife reserves and sanctuaries. The white-tailed deer, *Odocoilis virginianus*, is abundant on this island, with a density of approximately 27 deer/square kilometer (Myers, 1984). Additionally, mice were trapped on Conanicut Island, also situated in the Narragansett Bay, where there is no breeding population of white-tailed deer.

Three areas on Prudence Island (Fig. 5) were chosen for monthly sampling during May through November, 1987. These sites consist of South Prudence Management Area, Prudence Park and North Prudence Estuarine Sanctuary. The sampling areas are wooded habitats with mixed moist deciduous upland forest dominated by oak (*Quercus* sp.), red maple (*Acer rubrum*), black cherry (*Prunus serotina*), and a dense undercover of green briers (*Smilax* sp.), arrow wood (*Viburnum recognitum*), bayberry (*Myrica pensylvanica*), poison ivy (*Rhus radicans*) and bittersweet (*Celastrus scandens*).

To determine nymphal abundance and ERI, nymphal host-seeking ticks were collected by flagging a one meter square white flannel flag over the vegetation and ground cover. The number of host-seeking nymphs per person per hour is used here to denote tick abundance. Nymphs collected in the field were placed in glass vials with a gauze cover. Vials were placed in a plastic bag with a piece of moist cotton to supply moisture before

transportation back to the laboratory. In the laboratory, the vials containing ticks were placed in a humid chamber (90-100% Relative Humidity) at room temperature (21^0 C). Mathematically, ERI is the proportion of infected ticks multiplied by the number of ticks collected per sample (exposure) time. This index expresses the risk of encountering infected ticks in a particular time frame and in a defined area.

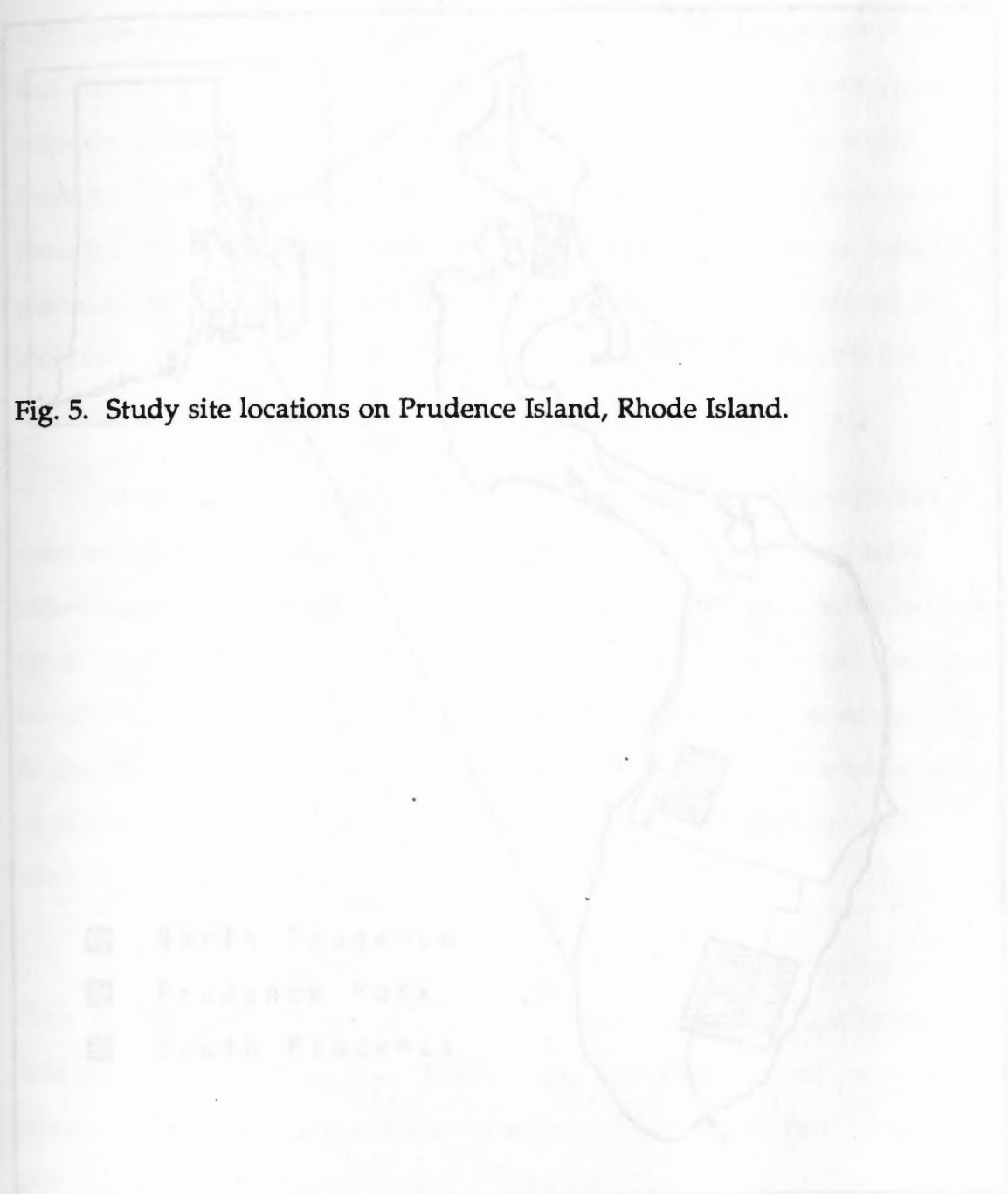
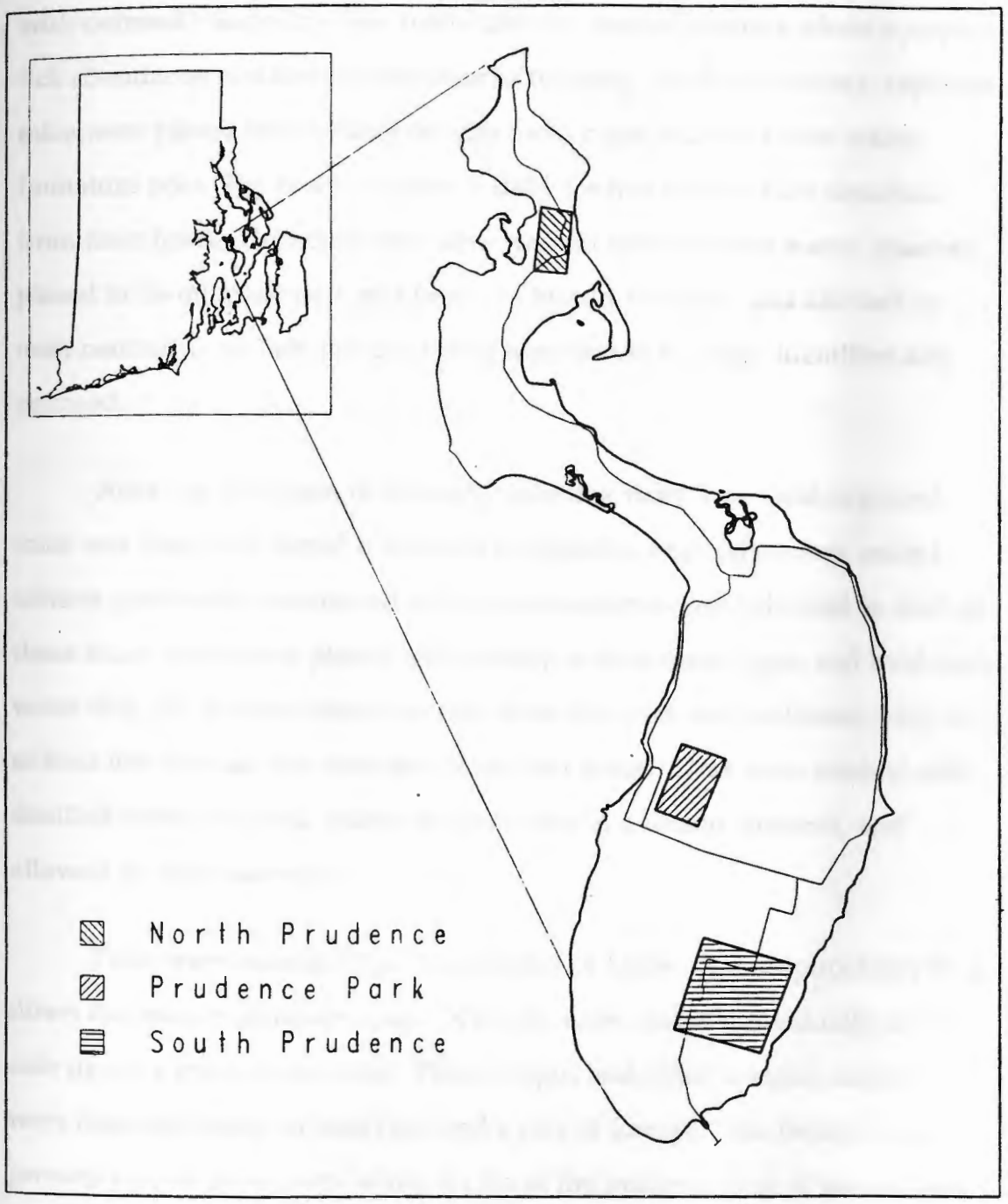


Fig. 5. Study site locations on Prudence Island, Rhode Island.


North Prudence
Prudence Park
South Prudence

To study the infestation rates of mice with immature deer ticks and their infectivity to larval ticks, mice from the three sampling areas were live-trapped using large folding Sherman box traps (23.2 X 9.0 X 7.7 cm) baited with oatmeal. Sampling was undertaken in similar habitats where nymphal tick abundance was determined prior to trapping. In the laboratory, captured mice were placed individually in wire mesh cages and held over water. Immature ticks (Fig. 6) were collected daily for five days as they detached from their hosts. Collected ticks were washed with distilled water, counted, placed in 24-ml glass vials and kept in a humid chamber, and allowed to molt naturally. Molted and dead ticks were sorted by stage, identified and counted.

After the collection of naturally-infesting ticks from field-captured mice was complete, larval *I. dammini* originating from laboratory reared cohorts previously determined to be spirochete-free, were allowed to feed on these mice. Mice were placed individually in wire mesh cages and held over water (Fig. 7). Replete immature ticks from the mice were collected daily for at least five days as they detached from their hosts. Ticks were washed with distilled water, counted, placed in glass vials in a humid chamber, and allowed to molt naturally.

Ticks were examined for the presence of Lyme disease spirochetes by a direct fluorescent antibody assay. Nymphs were placed individually dorsal side up on a microscope slide. Their midgut and other internal contents were dissected using an insect pin and a pair of forceps. The forceps were pressed against the scutum while the tip of the posterior part of the tick was punctured by the insect pin. The internal organs were squeezed into a drop

of sterile phosphate buffered saline (PBS) (0.1 M NaH_2PO_4 and 0.2 M Na_2HPO_4) and the exoskeleton pushed aside. A coverslip was placed on the viscera and compressed against the slide. The coverslip was removed, the preparation was allowed to air dry, fixed in acetone and stored in a freezer (-20^0 C) for future examination. For direct fluorescent antibody assay (DFA) slides were placed in a humid chamber for 15 min. A polyclonal rabbit anti-*B. burgdorferi* antibody conjugated with fluorescein isothiocyanate at a 1:100 dilution was added (20-36 µl per slide) and slides were then incubated for 30 min. at 37^0 C. Slides were then rinsed, washed for 30 min. with PBS, laid on dry paper towels, and a drop of PBS/glycerin (1:9) added to each slide and covered by a coverslip. Finally, slides were examined at 400X using fluorescence microscopy.

The number of infected ticks derived from mice and the number of collected ticks infesting mice (by stage and site) were analyzed relative to each month of sampling period. Arcsin transformation was performed on the infectivity data prior to ANOVA analysis. ANOVA was employed to analyze infectivity rates with respect to area and seasonal infestation of mice with tick.

Fig. 6. White-footed mouse, *Peromyscus leucopus*, parasitized with immature stages of *Ixodes dammini*

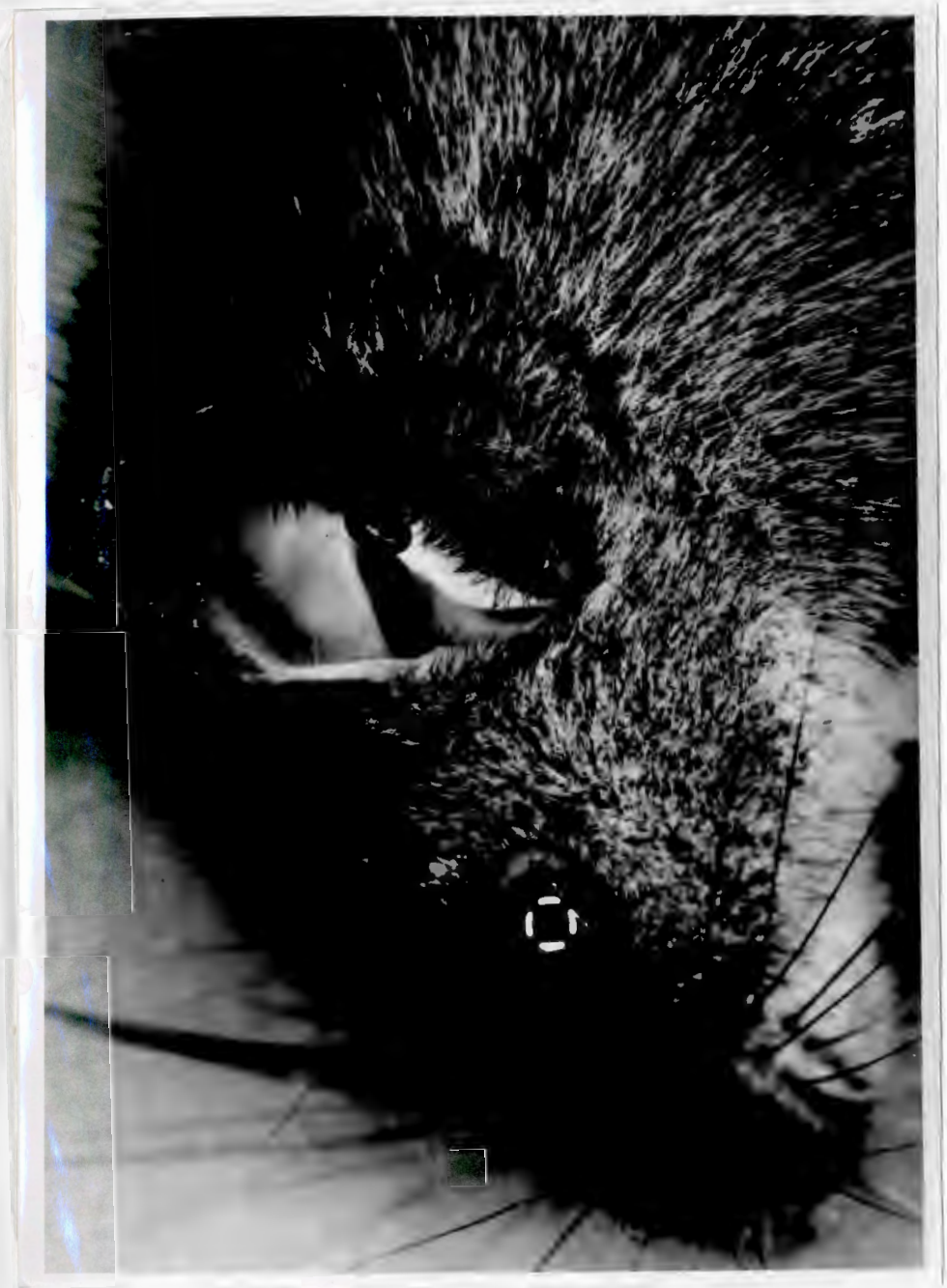
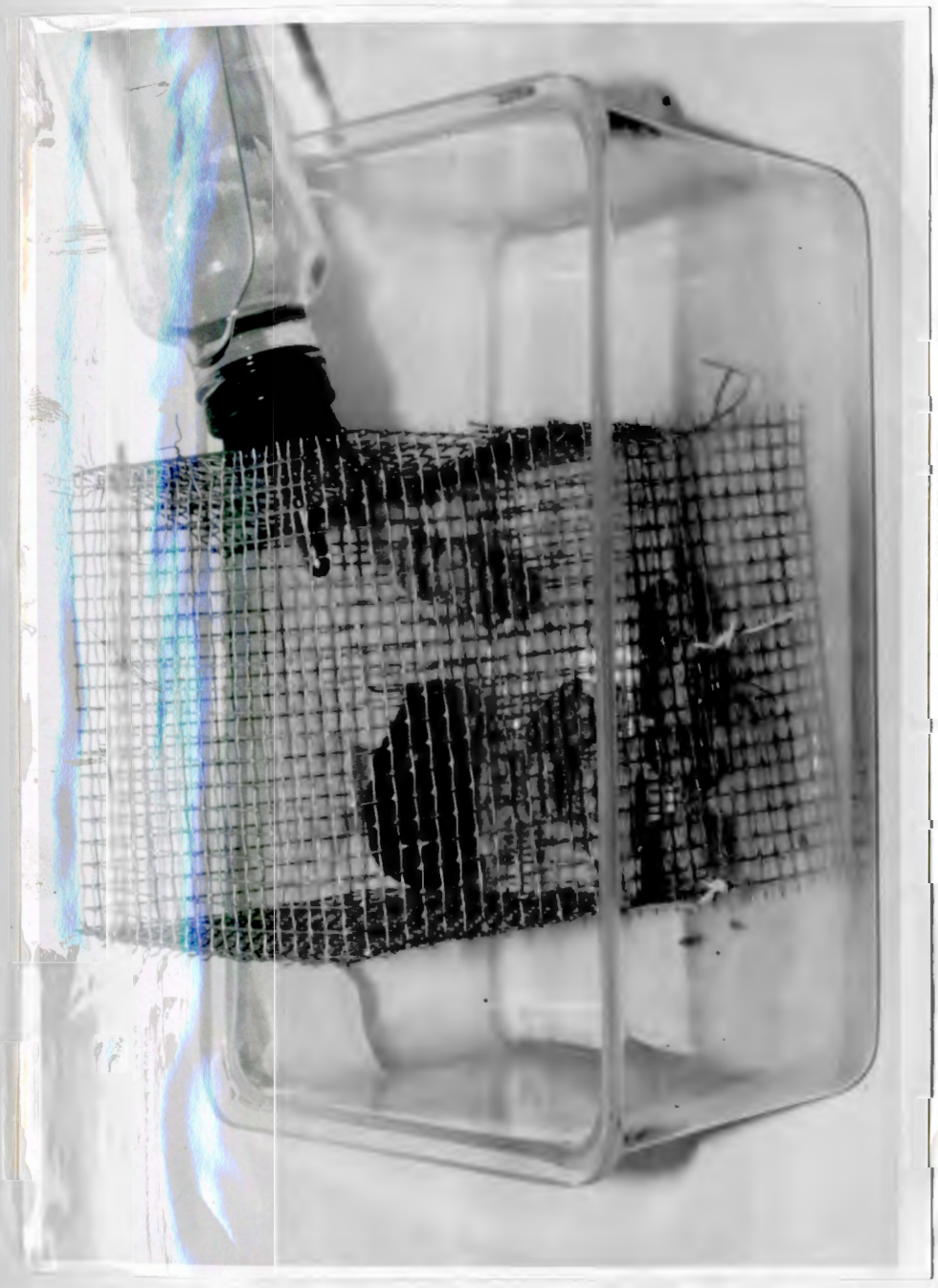


Fig. 7. *Peromyscus leucopus* held over water in a wire-mesh cage



RESULTS

Tick abundance varied from 8 to 32 nymphs per hour of flagging during May and August, 1987 at North Prudence (Table 3). Infection rate ranged from a low of 35.0% in May to 41.6% in June (Average 38.53 ± 1.45 (SE). ERI was highest in May (11.2), declined to 3.0 in August and was nil beginning in September because nymphs were absent during the months of September, October and November.

A total of 133 nymphs per person per hour was recovered during May from Prudence Park site (Table 4). Twenty-five of this stage were examined for the presence of *B. burgdorferi* of which 32% were infected, yielding a corresponding Entomological Risk Index of 42.56. In June, 73 nymphal ticks per person per hour were collected with an infection rate of 45% and an ERI of 32.4. Of 20 nymphs examined in July (78 total nymphs), seven were infected, resulting in an ERI of 27.3. An infection rate of 40% was found among nymphs flagged during August and giving an ERI of 15.6. No nymphs were encountered during the months of September, October and November. The average infection rate was 38% ± 2.86 (SE) from May through August.

At South Prudence Park the Entomological Risk Index varied from 66.0 in May to 8.4 in August (Table 5). The number of nymphal ticks collected during this time also varied between 30 and 165, with the greatest number sampled in May. Infection rates ranged from 30 to 45 %. No nymphs were collected from August through November.

Table 3

Entomological Risk Index and Nymphal *Ixodes dammini* Obtained at North Prudence, Prudence Island, 1987.

Month	Flagged Nymphs per person/hour	No. Examined	No. Infected	Infection Rate (%)	Entomological Risk Index (ERI)
May	32	20	7	35.0	11.2
June	22	12	5	41.6	9.6
July	20	15	6	40.0	8.0
August	8	8	3	37.5	3.0
September	0	0	0	0	0

Table 4

Entomological Risk Index and Nymphal *Ixodes dammini* Obtained at Prudence Park, Prudence Island, 1987.

Month	Flagged Nymphs per person/hour	No. Examined	No. Infected	Infection Rate (%)	Entomological Risk Index (ERI)
May	133	25	8	32	42.56
June	73	20	9	45	32.4
July	78	20	7	35	27.3
August	39	20	8	40	15.6
September	0	0	0	0	0

Table 5

Entomological Risk Index and Nymphal *Ixodes dammini* Obtained at South Prudence, Prudence Island, 1987.

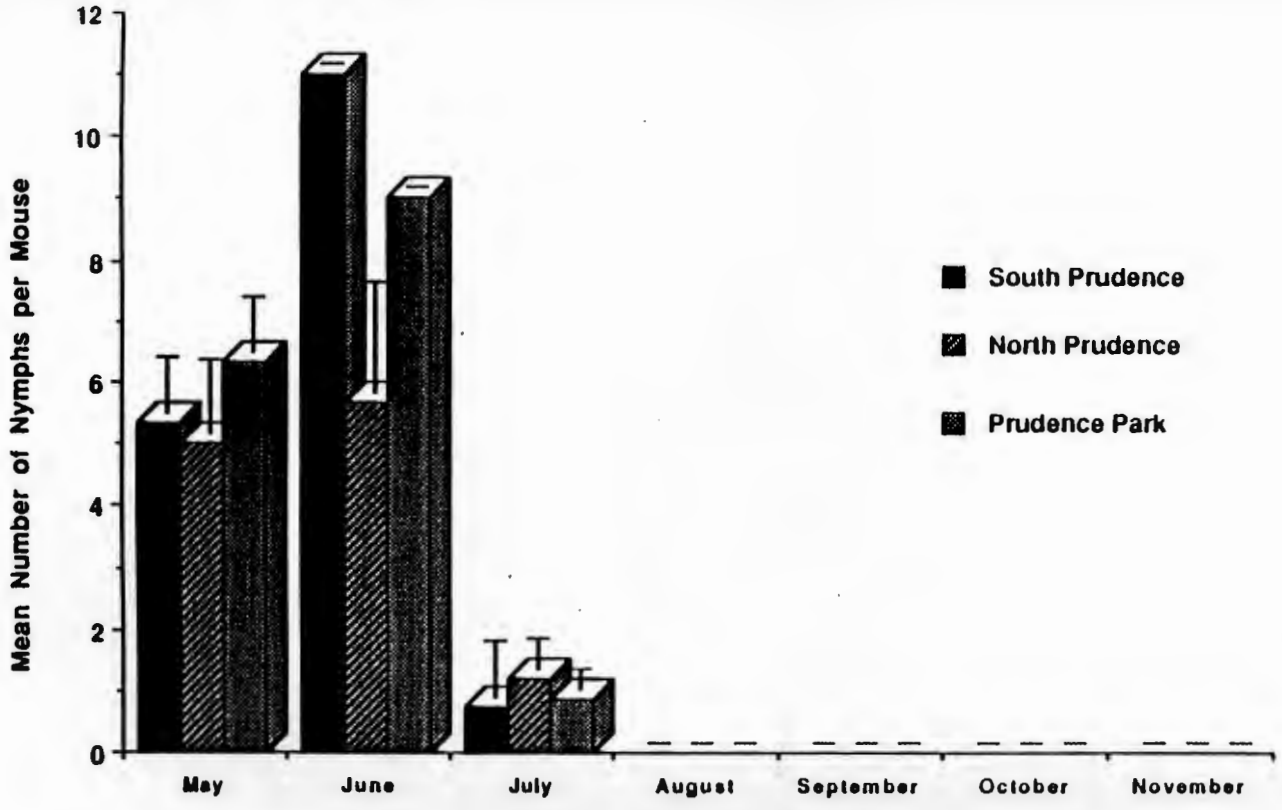
Month	Flagged Nymphs per person/hour	No. Examined	No. Infected	Infection Rate (%)	Entomological Risk Index (ERI)
May	165	25	10	40	66.0
June	86	20	9	45	38.7
July	58	20	8	40	23.2
August	28	20	6	30	8.4
September	0	0	0	0	0

A total of 114 mice were live-captured as follows (Appendices 1 to 3): South Prudence Park (40), Prudence Park (40) and North Prudence Park (34). Mice trapped from South Prudence Park showed an average of 5.3 ± 0.91 (SE), 11.0, and 2.0 ± 0.73 (SE) nymphs during May, June, and July respectively (Fig. 8). No nymphal ticks were recovered from mice examined in August to November. Infestation rates by larval *I. dammini* were 4.2 ± 0 .98 (SE) per mouse in May, 12.0 in June, 32.3 ± 9.90 (SE) in July, 37.8 ± 11.49 (SE) in August, 26.0 ± 6.98 (SE) in September, 8.83 ± 1.74 (SE) in October. Rates of infestation among mice trapped from South Prudence were shown to be significantly different (ANOVA, $P < 0.0001$) during the sampling months (Appendix 4).

Nymphal infestation rates among mice collected from Prudence Park (Fig. 8) were 6.3 ± 0.92 (SE) per mouse, 9.0 , 0.85 ± 0.34 (SE) from May to July. Mice were not parasitized by nymphs from August through November. However, larval infestation rates ranged from as low as 5.77 ± 2.7 (SE) in May to a high of 46.0 ± 5.00 (SE) in August (Fig. 9). Larval and nymphal tick infestation rates among mice collected from Prudence Park also changed significantly during the sampling period were significant, $P < 0.0002$ and < 0.0001, respectively (Appendix 5).

At North Prudence Park, the nymphal tick infestation rates ranged from 1.2 ± 0.48 (SE) in July to 5.66 ± 1.85 (SE) in June. No nymphs were recovered from August through November. Infestation rates by larval ticks varied from as low as 2.14 ± 0.96 (SE) per mouse in October to as high as 44.0 in July. No larval ticks infested mice in November. The abundance of immature deer ticks infesting mice changed significantly throughout the

Fig. 8. Seasonal abundance of nymphal *Ixodes dammini* infesting white-footed mice from three sites on Prudence Island, Rhode Island, 1987.


Mean Number of Nymphs per Mouse
12
10
8
6
4
2
0
May
June
July
August
September
October
November
South Prudence
North Prudence
Prudence Park

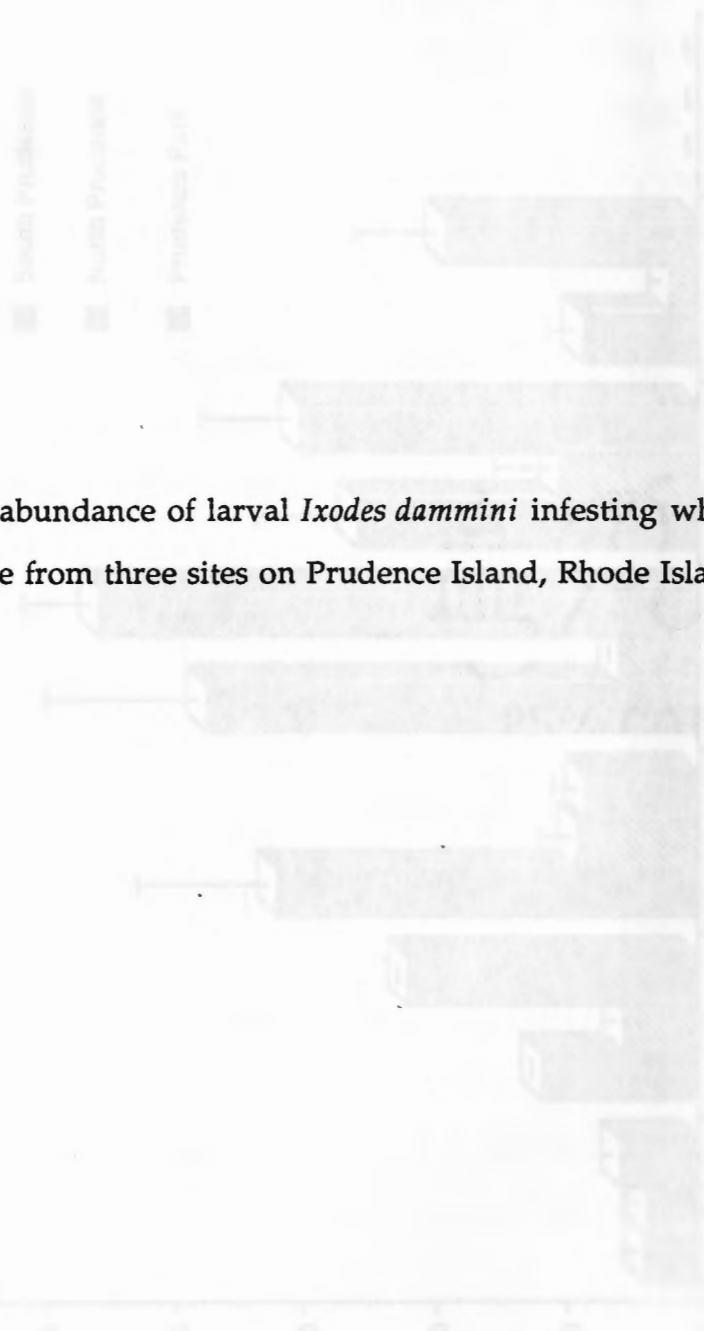
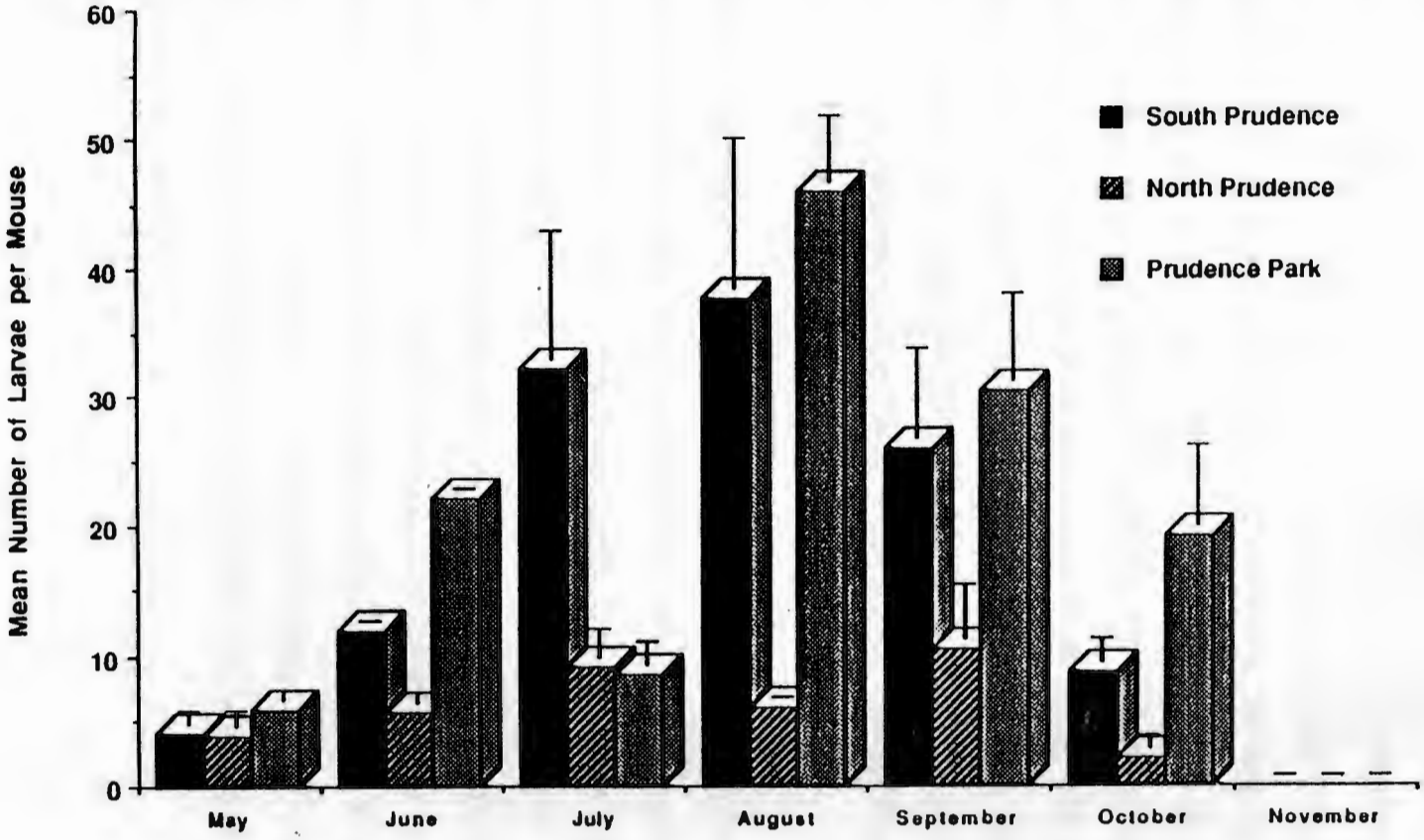


Fig. 9. Seasonal abundance of larval *Ixodes dammini* infesting white-footed mice from three sites on Prudence Island, Rhode Island, 1987.

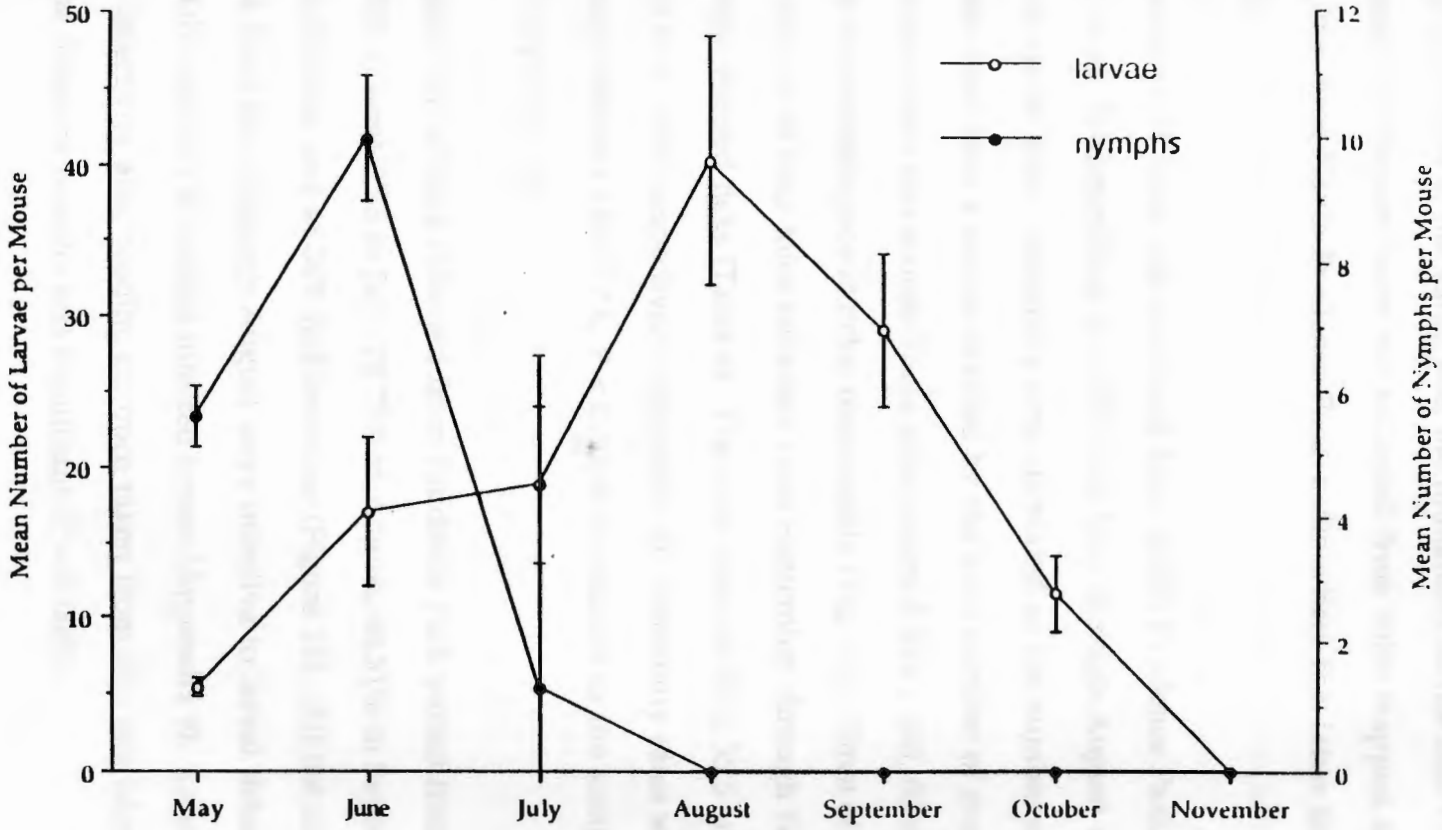

Mean Number of Larvae per Mouse
60
50
40
30
20
10
0
May
June
July
August
September
October
November
South Prudence
North Prudence
Prudence Park

study period($P < 0.0002$) for both larval and nymphal ticks (Appendix 6).

There were also no significant differences between the sites in the abundance of larvae infesting mice in May, August and September (P = 0.3647 and 0.1717, respectively, for all sites during May and September and 0.6902 for South Prudence and Prudence Park in August), while infestations were significant from all sites during October (P = 0.0063). No comparison was undertaken for June due to the number of mice trapped (2, 1, and 1 mice from South Prudence, Prudence Park and North Prudence, respectively). However, the overall infestation during the course of the study was not significantly different between South Prudence and Prudence Park sites (Fisher PLSD = 6.904), but there was a significant difference between South Prudence and North Prudence (Fisher PLSD = 7.301) and between Prudence Park and North Prudence (Fisher PLSD = 7.219).

In order to monitor the seasonal activity of larval and nymphal ticks infesting mice, South Prudence and Prudence Park results were combined for each month (Fig. 10). Mice trapped from North Prudence Park were not included because of the relatively high variation in infestation rates. The Combined average larval infestation on mice was 5.4 ± 0.582 (SE) in May, 17.0 ± 5.00 (SE) in June, 18.78 ± 5.27 (SE) in July, 40.14 ± 8.15 (SE) in August, 29.0 ± 5.01 (SE) in September, 11.63 ± 2.55 (SE) in October and 0 in November. Average nymphal deer tick infestation was 5.58 ± 0.48 (SE) in May, 10.0 ± 1.00 (SE) in June, 1.29 ± 5.271 (SE) in July, but no nymphs infested mice in August through November samples.

Fig. 10. Cumulative seasonal abundance of immature *Ixodes dammini* from two sites, South Prudence and Prudence Park, on Prudence Island, Rhode Island, 1987.


larvae
nymphs
Mean Number of Larvae per Mouse
Mean Number of Nymphs per Mouse
0
10
20
30
40
50
0
2
4
6
8
10
12
May
June
July
August
September
October
November

Ixodes dammini was the dominant tick species derived from trapped *P. leucopus*. Although 24 larval and 11 nymphal *Dermacentor variabilis* ticks were recovered at the study site, the immatures of the lone star tick, *Amblyomma americanum*, were not collected from mice trapped at any of the sites, including North Prudence Park, a site where this latter tick was abundant.

A total of 35 mice was examined from South Prudence Park. All mice collected South PrudencePark (n = 35) from May through August were infective to larval ticks. Infectivity was calculated as the number of infected nymphs derived from a mouse divided by the total number of examined nymphs taken from that mouse.These mice infected 90.6 , 100, 80 and 79 percent of the xenodiagnostic ticks, respectively (Fig. 11). Three of four, five of nine and one of four mice collected from September through November, respectively, infected ticks (Table 6). The mice infected 58.0, 35.5 and 35.8 percent of their ticks, respectively (Appendix 8). Infectivity rates were significantly different (ANOVA, $P < 0.0004$) in relation to the sampling months (Appendix 11).

Infectivity of mice collected from Prudence Park varied from 85.9% in May, 89.5% in June, 73.8 in July, 78.75% in August, 44.51% in September, 38.19% in October and 44.36% in November (Figure 11). All the mice examined from May through August were infective to larval ticks while 66.7%, 60.0% and 66.7% yielded infected larvae (Appendix 9). Larval *I. dammini* infectivity after feeding on mice taken from this site (Appendix 11) during the different months was significant ($P = 0.0081$).

Mice trapped at North Prudence showed infectivity rates of 87.2% in May, 70.5% in June, 68.8% in July, 83.3% in August, 25.1% in September, 27.7% in October and 30.2% in November (Fig. 11). All mice trapped from May throughout August were infective, while 33.3%, 40% and 50% of those trapped in September through November, respectively, were capable of infecting larvae (Table 6, Appendix 10). Infectivity of mice to larval ticks throughout the study period (Appendix 11) was significant (P = 0.0194).

A total of 18 mice collected from May through August on Conanicut Island was also examined. Two mice were infested with *I. dammini* larvae in June (1 larva) and August (1 larva). Otherwise, these mice were either infested by the American dog tick, *Dermacentor variabilis*, or were free of any tick infestation. All laboratory fed *I. dammini* larvae derived from these mice were spirochete-free (Table 6).

Juvenile mice trapped at all three Prudence Island sites from September to November were not infective to larval *I. dammini*, although juveniles taken during July and August from the same sites were infective but to varying degrees (83.3% in August at North Prudence, 40% and 58.8% during July at Prudence Park and 63.1 and 78.5% in July at South Prudence). Despite this, the overall infectivity of mice trapped from all sites on Prudence Island during the entire study period did not differ significantly (P = 0.5235).

Fig. 11. Seasonal infectivity of *Ixodes dammini* with *Borrelia burgdorferi* infecting white-footed mice trapped from three sites on Prudence Island, Rhode Island, 1987.

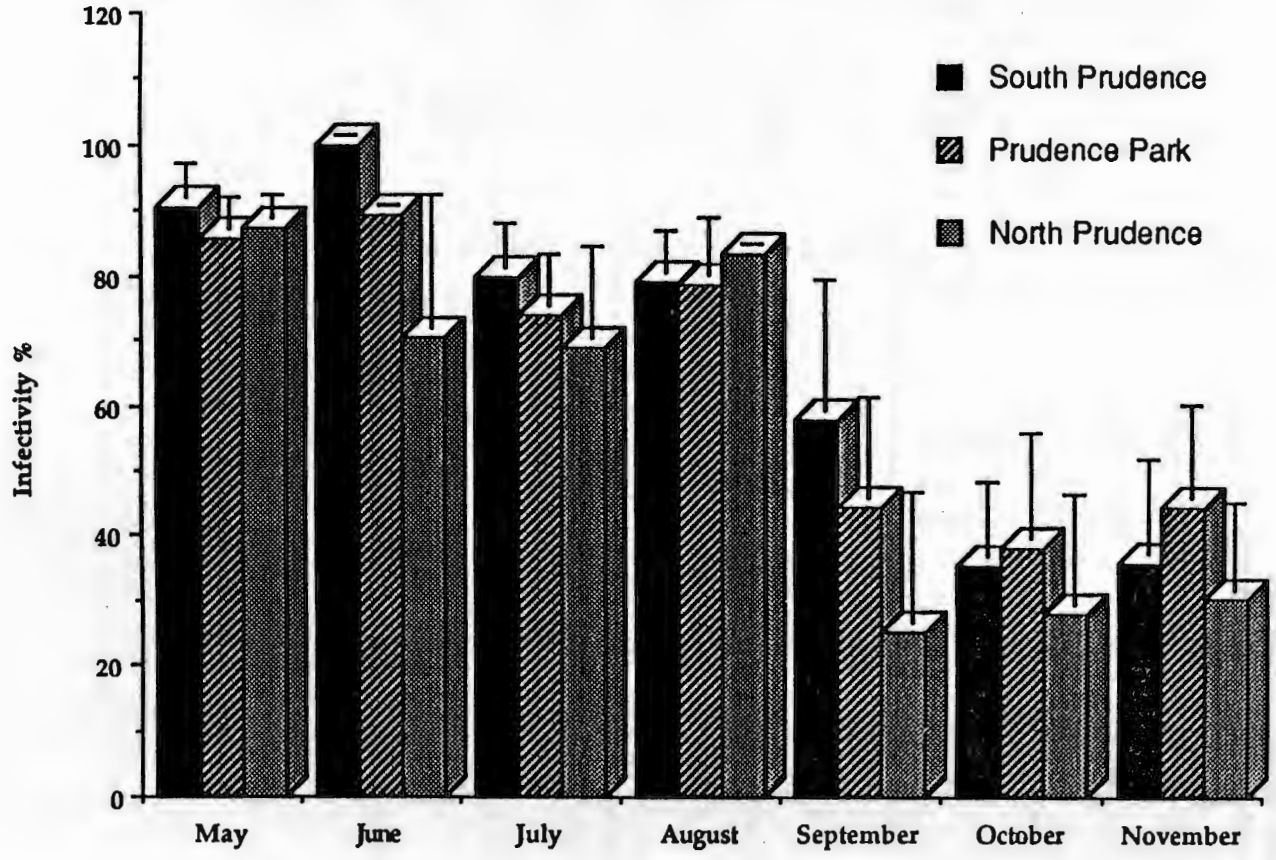

120
100
80
60
40
20
0
Infectivity %
South Prudence
Prudence Park
North Prudence
May
June
July
August
September
October
November

Table 6

Spirochetal (*B. burgdorferi*) Infectivity of White-footed Mice to Larval *I. dammini*

Month	Site	No. of mice examined	% infecting ticks	Distribution of individual infectivity (Percent of each cohort infected) <25%	26-50%	51-75%	>75%
May	South Prudence	6	100	0	0	1	5
	Prudence Park	9	100	0	0	2	7
	North Prudence	5	100	0	0	0	5
	Conanicut Island	5	0	5	0	0	0
June	South Prudence	1	100	0	0	0	1
	Prudence Park	1	100	0	0	0	1
	North Prudence	3	100	1	0	0	2
	Conanicut Island	4	0	4	0	0	0
July	South Prudence	6	100	0	0	2	4
	Prudence Park	7	100	0	1	3	3
	North Prudence	4	100	0	1	1	2
	Conanicut Island	4	0	4	0	0	0
Aug	South Prudence	5	100	0	0	1	4
	Prudence Park	2	100	0	0	1	1
	North Prudence	1	100	0	0	0	1
	Conanicut Island	5	0	0	0	0	0
Sept	South Prudence	4	75	1	0	1	2
	Prudence Park	6	66.7	2	1	1	2
	North Prudence	3	33.3	2	0	1	0
Oct	South Prudence	9	44.4	4	0	4	1
	Prudence Park	5	60	2	0	3	0
	North Prudence	5	40	3	0	2	0
Nov	South Prudence	4	75	1	2	1	0
	Prudence Park	6	66.7	2	0	3	1
	North Prudence	6	50	3	0	3	0

DISCUSSION

Human infection is caused primarily by the bite of a *B. burgdorferi*-infected nymphal deer tick (Spielman et al., 1985; Matuschka and Spielman, 1986). However, female ticks may also transmit spirochetes during the fall and winter or whenever they are active (Schulze et al., 1985). Larval *I. dammini* play no major role in the epidemiology of this disease since transovarial transmission is very low (Piesman et al., 1986; Magnarelli et al., 1987). Thus, determining nymphal tick abundance is an appropriate and practical measure for describing the risk for *B. burgdorferi* transmission to human populations during late spring and mid-summer.

The role of other tick species in *B. burgdorferi* transmission is controversial. *Borrelia burgdorferi* has been detected in or isolated from the lone star tick, *Amblyomma americanum*. In New Jersey, Schulze et al. (1984a) isolated *B. burgdorferi* from specimens recovered from patients who developed characteristic Lyme disease ECM. Moreover, they found 9.1% of field collected nymphal and adult *A. americanum* carrying the spirochete. Magnarelli et al. (1986a) detected the spirochete in 3.5% of 173 lone star ticks taken from North Carolina. Also, Rawlings (1986) isolated *B. burgdorferi* from *A. americanum* specimens collected in Texas.

Additionally, the spirochete was identified from the pre-adult American dog tick, *Dermacentor variabilis*, feeding on white-footed mice (Anderson et al., 1985; Anderson et al., 1987c). Rawlings (1986) reported on unidentified spirochetes isolated from *D. variabilis* in Texas. Moreover, *Rhipicephalus sanguineus* and *Dermacentor parumapertus* were found

infected with *B. burgdorferi* (Rawlings, 1986), in eastern Texas where *R. sanguineus* is common.

Recently, Piesman and Sinsky (1988) showed that larval *A. americanum* from Alabama were capable of acquiring the spirochete, but that the ticks did not maintain *B. burgdorferi* and pass it transstadially. Likewise, ticks originating from Texas failed to acquire the Lyme disease spirochete. In a separate study, a total of 179 nymphal *A. americanum* collected from Prudence Island were examined for the presence of *B. burgdorferi*. All nymphs were spirochete-free (Hyland, personal communication).

Nymphal deer tick abundance varied among the three different study sites throughout the study period. South Prudence Park showed the highest nymphal population in May and June (165 and 86 nymphs per hour, respectively). Nymphal abundance at Prudence Park was also high from May to August (133 and 39 nymphs per hour). The lowest level of tick abundance was observed at North Prudence where just 8 to 32 nymphs were collected per person per hour from May to August.

Variation in nymphal tick abundance among the three study sites is perhaps related to the relative abundance of white-tailed deer. Deer were encountered more often at South Prudence Park, were seen less frequently at the Prudence Park and were never encountered at North Prudence Park. Additionally, deer fecal pellets were more frequent at South Prudence and Prudence Park compared to North Prudence Park. Wilson et al. (1985) showed that observation of "pellet groups" provides an index to the relative

density of the white-tailed deer which could be correlated with the abundance of larval but not to nymphal ticks.

Average infection rates among the three site for the nymphal season were similar: Prudence Park (38%), North Prudence (38.52%) and South Prudence (36.25%). This indicates an even distribution of the infected reservoir host, *P. leucopus*, throughout the island. At the three sites studied, South Prudence Park had the highest ERI. This may be due to the relative abundance of host-seeking nymphs and the high density of spirochete-infected reservoir hosts (i.e. *P. leucopus*). On the other hand, North Prudence Park showed a lower ERI, which may be due to the lower populations of both white-tailed deer and the presence of high levels of the lone star tick, *A. americanum*. Variation in density of *I. dammini* populations has been observed by several workers (Anderson et al., 1983; Anderson et al., 1987b; Piesman et al., 1987; Falco and Fish, 1988a; 1988b). This is perhaps due to the availability and abundance of infected competent reservoir hosts.

The Entomological Risk Index described and used herein can provide health officials and other concerned authorities with information to base control or treatment strategies in particular areas. By itself, ERI gives a numerical value for the possibility of being bitten by spirochete-carrying nymphal *I. dammini*. Other measures of risk, namely encounter distance, as proposed by Falco and Fish (1989a) fail to include the proportion of *Borrelia* infected ticks, providing just a numerical value for the tick density per unit area. This latter measure would also need to define the type of habitat being

sampled. An "encounter distance" obtained in grassy habitat might not accurately reflect risk in other types of habitat at the same site.

From January to September 1989, a total of 291 Lyme disease cases were reported to the Rhode Island Department of Health (Dr. E. Jost, personal communication). The higher frequencies (Fig. 12) of diagnosed cases were seen during May (49), June (92) and July (67). The onset of the clinical manifestation of Lyme disease corresponds with the ERI. Winter cases may be attributed to bites by adult females (Schulze et al., 1985). Transmission of Lyme disease is highest during May to July, coinciding with the peak season for nymphal *I. dammini*, and the number of reported human cases. Outdoor activities should be undertaken with care during these months.

Ginsberg and Ewing (1989b) studied habitat distribution of *I. dammini* on Fire Island, New York. They indicated that questing nymphs and larvae were very abundant in wooded areas, especially in leaf litter, rather than open grassland habitats. However, the number of immatures parasitizing the white-footed mice was not significantly different in various types of habitats. Adult ticks were more common on high shrub habitat (about one meter above ground level) rather than in grassy or low shrub habitats. Similar observation were made on Prudence Island during the course of this study.

Different control alternatives should also be considered before, during and after late summer. These include mowing or burning vegetation, spraying acaricides on undercover vegetation and leaf litter in high use areas of high risk and the use of acaricides that target attached ticks on mice to

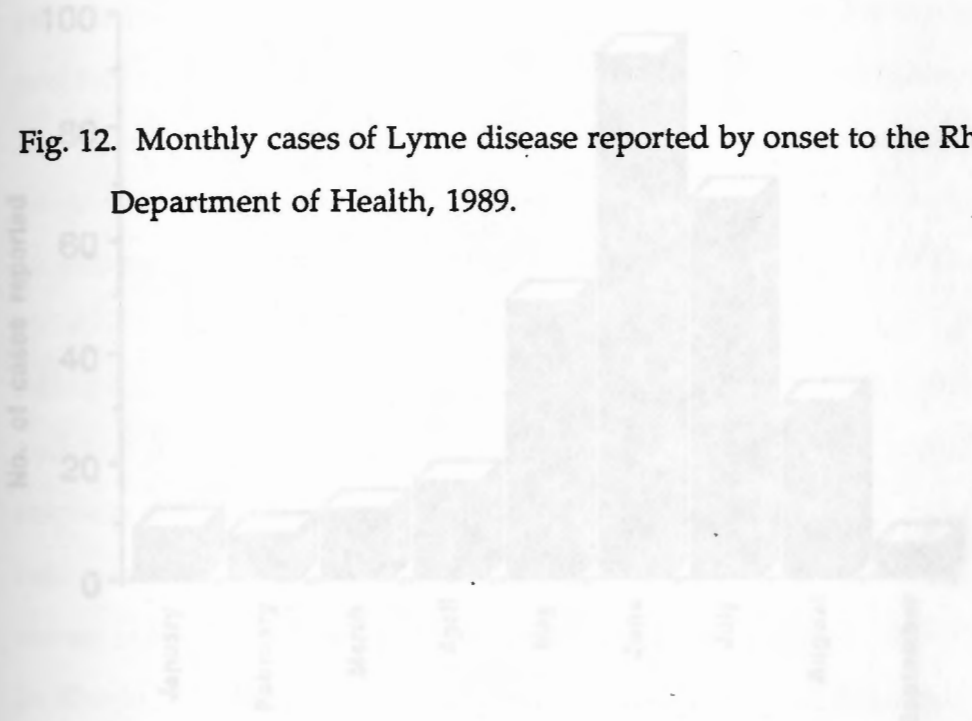
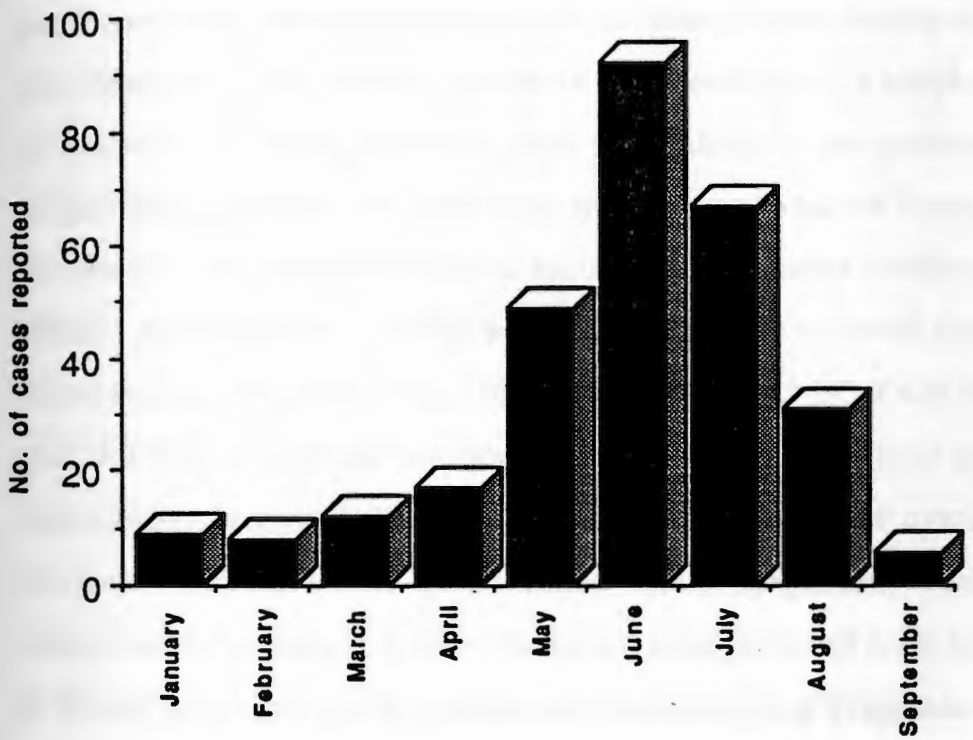


Fig. 12. Monthly cases of Lyme disease reported by onset to the Rhode Island Department of Health, 1989.


100
80
60
40
20
0
No. of cases reported
January
February
March
April
May
June
July
August
September

reduce the number of spirochete-infected nymphs in the following season (Mather et al., 1987). Efforts in educating the public to avoid high risk areas should be undertaken by posting warning signs.

Previous studies have shown that Prudence Island is a focus for Lyme disease (Anderson and Magnarelli, 1983; Anderson et al., 1986b; Anderson et al., 1987d; Magnarelli et al., 1988). However, these investigations were short-termed and were not conducted on a regular basis. Anderson and Magnarelli (1983) reported an average of six (SD ±1.2) larvae of *I. dammini* per mouse from samples collected from Prudence Island during September and November, 1982. Spirochetes were recovered from the blood of one of 20 trapped mice. Nine of 22 mice were seropositive for the presence of *B. burgdorferi* antibodies. Of seven mice trapped on the island during November, 1984, six were found to harbor the spirochetes (Anderson et al., 1986b). Anderson et al. (1987d) examined *P. leucopus* collected from this island during 1984-1985. They found an average of 3.3 (SD ± 4.0) nymphs and 13.0 (SD±14.2) larvae per mouse during the months of June and August, respectively. Moreover, 33 of 129 attached larvae and 6 of 20 nymphs recovered from these mice were infected with *B. burgdorferi*. Twenty-five serum samples obtained from white-footed mice collected from inland areas in Rhode Island and Block, Conanicut (Jamestown) and Prudence Islands revealed an infection rate of 20% when examined using ELISA and 12% when utilizing IFA (Magnarelli et al., 1988).

Differences in infestation rates among mice within the same site are perhaps due to the clustering behavior exhibited by *I. dammini* larvae. After feeding on deer or other medium or large-sized animals, the replete female deer tick drops to the forest floor and oviposits. Hatched larvae tend to

cluster near the site of oviposition. While foraging at night, white-footed mice may encounter such clusters, resulting in a higher infestation rate than those mice which did not encounter such clusters. Mice trapped from South Prudence Park were heavily infested with larval deer ticks (32.33, 37.80 and 26.00 during July, August and September), while mice taken from Prudence Park were less infested for the months of July (8.62) and September (30.50). Mice collected from North Prudence had the least number of larvae in July and September.

Tick abundance on *P. leucopus* is perhaps related to mouse densities and home range. Indeed, home range may be an important factor in determining mouse infestation rates with immature *I. dammini*, especially with the larvae. White-footed mice have a home range of 634 m^2 and 511 m^2 for males and females, respectively (Wolff 1986). Such home range may explain variations in the number of immature ticks depending on their spatial distribution in a particular location. Moreover, fluctuations in *P. leucopus* population density vary from one season and one year to another. According to Metzgar (1971) these fluctuations can be attributed to behavioral territoriality of both sexes of this mouse species.

Additionally, mouse infestation rates are related to the density of white-tailed deer. Wilson et al. (1985) stated that "pellet group" provides an index to the relative density of the white-tailed deer in relation to larval but not for the nymphal tick abundance. More deer fecal pellets were observed at the South Prudence site compared to North Prudence Park. No attempts were made to quantify these observations.

Godsey et al. (1987) suggested that differences in the number of ticks per mouse may be related to trapping procedures and that tick abundance varies yearly. Larval densities on white-footed mice trapped from the three study sites on Prudence Island were higher than those reported from mice examined in Connecticut (Main et al., 1982; Anderson and Magnarelli, 1984), and Wisconsin (Godsey et al., 1987). Averages higher than 12 larvae per mouse were recorded from Nantucket Island, Massachusetts (Piesman and Spielman, 1979) and Shelter Island, New York (Bosler et al., 1983).

Owing to the high number of larvae attached and feeding on mice, it seems that *P. leucopus* is tolerant to the bites of *I. dammini* larvae. Immature deer ticks can feed repeatedly on this rodent species (Spielman, 1988). The low number of American dog ticks parasitizing mice on Prudence Island does not imply that this rodent species may have become immune or refractory to *D. variabilis*.

Although Piesman and Spielman (1979), Wilson and Spielman (1985) and Wilson et al. (1985) proposed that larval *I. dammini* develop in a one season cohort, the sharp increase in larvae parasitizing *P. leucopus* during August and September (Fig. 5) suggests that those larvae hatched during the summer months. May and June larvae, however, are from the previous summer and represent those which survived the winter. Larval infestation rates increased several fold during July through September among mice trapped from the three sites. This is in agreement with the bimodal pattern suggested earlier by Main et al. (1982) and Spielman (personal communication).

Although gray squirrels and white-tailed deer were found to harbor a significantly high number of immature deer ticks, they are less abundant than white-footed mice in wooded areas. Main et al. (1982) reported an average of 13.8 larval and 27.3 nymphal *I. dammini* per squirrel in Connecticut. White-tailed deer were infested with an average of 342 larvae. The contribution of white-footed mice to the seasonal activity of *I. dammini* seems to be significant. In the study sites, this rodent species appears to be the most common species in wooded areas where these stages are abundant. This study demonstrates the contribution of *P. leucopus* in maintaining immature tick populations, where one mouse may host as many as 14.7 larvae per day from May to late October and 3.6 nymphs from May to August. Replete immature deer ticks detach from their hosts during the time of the day when the mice are in their burrows (Mather and Spielman, 1986). This finding is important in directing tick and Lyme disease control strategies as proposed by Mather et al. (1987).

Infectivity of white-footed mice captured from an endemic area to larval *I. dammini* can reveal the importance of the enzoonotic interaction between these two species in the epidemiology of Lyme disease in the Northeast. In the wooded habitat of all three Prudence Island study sites, *P. leucopus* was the only rodent species encountered. One specimen of the meadow vole, *Microtus pennsylvanicus*, was trapped from North Prudence.

White-footed mice are efficient reservoir hosts capable of infecting the immature stages of the deer tick. Mather et al. (1989b) suggested that reservoir competence may vary under different circumstances. In this study, mice were infectious to larval ticks where nymphal ticks, either host-seeking

or host-attached, were abundant. On Conanticut Island, where nymphal ticks were not observed, this reservoir species never infected larvae in a xenodiagnosis. An interesting further study would measure the level of host-seeking nymphal ticks necessary to result in infectious reservoir mice.

White-footed mice remained infective for the entire period of larval activity. Mice trapped during May and early summer were more infective to larval ticks possibly due to a higher spirochetemia caused by repeated exposure to host-seeking nymphal deer ticks that are in abundance during these months. This finding has epizootiological importance because larval ticks that feed on mice during the summer will emerge as nymphal ticks the following season, yielding a high proportion of spirochete infected nymphs that are capable of transmitting *B. burgdorferi*. Whether all infected ticks can retain the infection over the winter period should be investigated. Moreover, these findings are important in implementing plans for Lyme disease control strategies. Using cotton balls impregnated with insecticides (Mather et al., 1987) that are utilized in nest building by the white-footed mouse could certainly result in mortality of engorged larval ticks that have perhaps detached and dropped in the mouse nest (Mather and Spielman, 1986). Despite the variation in the number of host-seeking nymphs among the three study sites, differences in infectivity of mice taken from these locations to ticks was not significant. Donahue et al. (1987) exposed white-footed mice to various number of infected infected nymphs and found that a bite from one infected nymphal tick is sufficient to cause an infection in these mice and consequently these mice were infective to larval tick.

Ticks derived from white-footed mice were heavily infected with *B. burgdorferi*. This is perhaps attributed to the fresh infection of these ticks, which were maintained under laboratory conditions that allowed the spirochetes to multiply more readily rather than under field conditions. This observation is based on spirochetal infection sought among host-seeking nymphs flagged from the study sites, where the density of spirochetes per nymph was not as high as those seen in larval ticks that were collected from mice.

Juvenile mice trapped from September through November were not infective to larval ticks due to the absence of host-seeking nymphs during this period. The breeding cycle of *P. leucopus* extends from April to mid-November, with peaks in April, June, September and October (Wolff, 1986). Additionally, juveniles may acquire immunity from the female during gestation. Further studies are needed to explore this aspect of transplacental immunity. On the other hand, finding infected females during late summer and early fall suggests that spirochetes are not transmitted from mice females to their offspring.

Spielman et al. (1985) suggested that the Lyme disease spirochetes overwinter in nymphal *I. dammini*. However, it is possible, that *B. burgdorferi* can survive the winter in *P. leucopus*. Anderson et al. (1987b) isolated the spirochete year-round from white-footed mice. Other mammals, such as chipmunks, were found to infect larval *I. dammini*, but not as efficiently as white-footed mice (Mather et al., 1989a). Thus, these animals would likely serve as less efficient overwintering hosts.

Although contact transmission proposed by Burgess et al (1986) and Burgess and Patrican (1987) remains unconfirmed, immature *I. dammini* are the principal vector for *B. burgdorferi* transmission among mice and these mice, in turn, perpetuate the infection by infecting feeding vectors. None of the mice trapped from Conanicut Island were infested with nymphal deer ticks at the time of capture and none infected larvae feeding in a xenodiagnosis. This site was flagged during the summer on several occasions with no success in recovering host-seeking nymphs, In addition, Anderson et al. (1987b) obtained negative titers against *B. burgdorferi* for mice collected from this island. On the other hand, mice originating from Prudence Island were infective to ticks from May to November. The presence of host-seeking and host-attached nymphal *I. dammini* appears to be prerequisite for spirochetal infectivity among white-footed mice.

Susceptibility of vertebrate hosts to *B. burgdorferi* infection varies. Burgdorfer (1984) showed that rabbits became infected with the spirochete, however, this host lost its infectivity to ticks within two weeks post-infection. Hamsters, on the other hand, retained their infection and were able to infect *I. dammini* ticks for six months. Furthermore, infected white-footed mice remained infective to larval ticks for at least nine weeks after the initial infection (Donahue et al., 1987). The hispid cotton rat, *Sigmodon hispidus*, maintained the spirochetal infection for a maximum of four weeks (Burgdorfer and Gage, 1986). On the other hand, other species of hosts although infected, appear incapable of infecting ticks. White-tailed deer were heavily infested with all stages of *I. dammini*, less than 1% of detached larvae were infected with *B. burgdorferi* (Telford et al., 1988), suggesting that this host is incompetent to serve as reservoir. Likewise, Mather et al. (1989b)

demonstrated that catbirds were not incompetent reservoir hosts for Lyme disease spirochete. Further studies will be necessary to document the reservoir potential of other tick hosts.

ERI is useful to estimate the infected tick level in parks, recreational and high use areas as well as private properties in endemic regions. Leisure activities, including hiking, camping, hunting, and field-related occupations (military trainees, forestry rangers, naturalists, landscapers and wood cutters) result in high exposure to infected nymphs in woodlands. Prudence Island is considered a popular resort area for summer vacationers, and is a popular hunting ground for deer and game birds. Some of these activities are carried out during early summer, the time of the year when host-seeking nymphs are abundant. Hunting occurs in the Fall when the adults are active. Subsequent, control measures may be suggested and implemented to reduce the risk of transmission. Further studies should address the pattern of exposure and the incidence of Lyme disease infection among these groups.

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Appendix 1

Immature *Ixodes dammini* collected from mice trapped from South Prudence, Prudence Island, 1987.

Month	Mouse No.	Sex	No. of larvae	No. of Nymphs
May	1	M	4	9
May	2	F	3	4
May	3	F	6	7
May	4	M	2	3
May	5	M	8	5
May	6	M	2	4
June	7	M	12	11
July	8	M	36	5
July	9	M	78	3
July	10	F	23	1
July	11	J	15	2
July	12	J	31	1
July	13	M	11	0
August	14	F	14	0
August	15	F	13	1
August	16	M	58	0
August	17	M	34	0
August	18	M	70	0
September	19	F	15	0
September	20	M	36	0
September	21	M	40	0
September	22	J	13	0
October	23	J	8	0
October	24	J	11	0
October	25	M	2	0
October	26	M	12	0
October	27	F	15	0
October	28	M	14	0
October	29	M	2	0
October	30	J	4	0
October	31	F	18	0
October	32	J	15	0
October	33	J	1	0
October	34	M	4	0
October	35	F	11	0
November	36	M	0	0
November	37	M	0	0
November	38	M	0	0
November	39	F	0	0
November	40	F	0	0

Appendix 2

Immature *Ixodes dammini* collected from mice trapped from Prudence Park, Prudence Island, 1987.

Month	Mouse No.	Sex	No. of larvae	No. of Nymphs
May	1	M	5	6
May	2	M	3	7
May	3	F	6	8
May	4	M	10	6
May	5	M	6	5
May	6	M	8	4
May	7	F	9	12
May	8	M	2	7
May	9	M	3	2
June	10	F	22	9
July	11	M	10	1
July	12	F	0	0
July	13	M	10	2
July	14	J	2	0
July	15	M	16	1
July	16	M	11	2
July	17	J	10	0
August	18	M	41	0
August	19	M	51	0
September	20	J	13	0
September	21	M	41	0
September	22	M	72	0
September	23	F	20	0
September	24	M	19	0
September	25	M	27	0
September	26	J	37	0
September	27	J	15	0
October	28	M	31	0
October	29	M	36	0
October	30	J	2	0
October	31	F	11	0
October	32	J	16	0
November	33	J	0	0
November	34	J	0	0
November	35	M	0	0
November	36	M	0	0
November	37	F	0	0
November	38	M	0	0
November	39	M	0	0
November	40	F	0	0

Appendix 3

Immature *Ixodes dammini* collected from mice trapped from North Prudence, Prudence Island, 1987.

Month	Mouse No.	Sex	No. of Larvae	No. of Nymphs
May	1	M	3	2
May	2	M	4	6
May	3	F	1	3
May	4	F	7	5
May	5	M	5	9
June	6	M	6	7
June	7	F	7	8
June	8	M	4	2
July	9	F	7	1
July	10	F	16	1
July	11	F	10	3
July	12	M	3	0
July	13	M	10	1
August	14	J	44	1
September	15	J	4	0
September	16	J	3	0
September	17	F	15	0
September	18	M	20	0
October	19	J	7	0
October	20	J	2	0
October	21	J	1	0
October	22	J	0	0
October	23	M	1	0
October	24	F	4	0
November	25	M	0	0
November	26	M	0	0
November	17	F	0	0
November	28	M	0	0
November	29	F	0	0
November	30	J	0	0
November	31	M	0	0
November	32	J	0	0
November	33	M	0	0
November	34	F	0	0

Appendix 4

Analysis of variance for South Prudence

Larval Stage

Source	DF	Sum of Squares	Mean Squares	F Value	PR < F
Model	5	7110.735	1422.147	6.89	0.0002
Error	32	6602.633	206.332		
Corrected Total	37	13713.368			

Nymphal Stage

Source	DF	Sum of Squares	Mean Squares	F Value	PR < F
Model	5	139.352	27.87	19.55	0.0001
Error	29	41.333	1.425		
Corrected Total	34	180.685			

Appendix 5

Analysis of variance for Prudence Park

Larval Stage

Source	DF	Sum of Squares	Mean Squares	F Value	PR < F
Model	5	6767.544	1353.508	12.21	0.0001
Error	34	3770.230	110.889		
Corrected Total	39	10537.775			

Nymphal Stage

Source	DF	Sum of Squares	Mean Squares	F Value	PR < F
Model	5	264.374	52.875	26.1	0.0001
Error	33	66.875	2.026		
Corrected Total	38	331.230			

Appendix 6

Analysis of variance for North Prudence

Larval Stage

Source	DF	Sum of Squares	Mean Squares	F Value	PR < F
Model	5	478.737	95.747	7.12	0.0002
Error	27	363.324	13.456		
Corrected Total	32	842.060			

Nymphal Stage

Source	DF	Sum of Squares	Mean Squares	F Value	PR < F
Model	5	158.715	31.743	15.45	0.0001
Error	27	55.466	2.054		
Corrected Total	32	214.182			

Appendix 7

Analysis of variance for three sites on Prudence Island

One Factor ANOVA

Larval Stage

Source	DF	Sum of Squares	Mean Squares	F Value	PR<F
Model	2	2193.25	1096.625	4.521	0.013
Error	110	26680.113	242.546		
Corrected Total	112	28873.363			

One Factor ANOVA
Nymphal Stage

Source	DF	Sum of Squares	Mean Squares	F Value	PR < F
Model	5	12.645	1.323	0.162	0.8504
Error	110	871.755	8.147		
Corrected Total	112	874.400			

Appendix 8

Infectivity of mice from South Prudence to larval ticks with *Borrelia burgdorferi*, 1987.

Month	Mouse No.	Sex	No. of Derived Nymphs	No. of Infected Nymphs	% Infectivity
May	1	M	19	16	84.21
May	2	F	18	18	100.00
May	3	F	14	14	100.00
May	4	M	19	19	100.00
May	5	M	20	14	70.00
May	6	M	19	17	89.47
June	7	M	20	20	100.00
July	8	M	16	14	87.50
July	9	M	20	18	90.00
July	10	F	16	16	100.00
July	11	J	14	11	78.57
July	12	J	19	12	63.15
July	13	M	18	11	61.11
August	14	F	20	17	85.00
August	15	F	16	10	62.50
August	16	M	19	18	94.73
August	17	M	17	11	64.70
August	18	M	17	15	88.23
September	19	F	19	15	78.90
September	20	J	18	0	0.00
September	21	M	17	15	88.23
September	22	M	20	13	65.00
October	23	J	15	0	0.00
October	24	J	17	0	0.00
October	25	M	16	9	56.25
October	26	F	20	15	75.00
October	27	M	14	8	57.14
October	28	M	18	12	66.66
October	29	J	18	0	0.00
October	30	F	17	11	64.70
October	31	J	15	0	0.00
November	32	M	20	14	70.00
November	33	M	18	6	33.33
November	34	F	15	6	40.00
November	35	J	16	0	0.00

Appendix 9

Infectivity of mice from Prudence Park to larval ticks with *Borrelia burgdorferi*, 1987.

Month	Mouse No.	Sex	No. of Derived Nymphs	No. of Infected nymphs	% Infectivity
May	1	M	13	13	100.00
May	2	M	17	15	88.24
May	3	F	14	10	71.43
May	4	M	17	16	94.12
May	5	M	15	9	60.00
May	6	M	18	17	94.44
May	7	F	20	20	100.00
May	8	M	20	17	85.00
May	9	M	20	16	80.00
June	10	F	19	17	89.50
July	11	M	20	12	60.00
July	12	F	20	17	85.00
July	13	M	12	11	91.67
July	14	J	10	4	40.00
July	15	M	15	13	86.67
July	16	M	20	19	95.00
July	17	J	17	10	58.82
August	18	M	16	14	87.50
August	19	M	20	14	70.00
September	20	M	19	16	84.21
September	21	M	17	13	76.47
September	22	F	17	11	64.71
September	23	M	12	5	41.67
September	24	J	13	0	0.00
September	25	J	19	0	0.00
October	26	M	20	13	65.00
October	27	M	19	10	52.63
October	28	J	16	0	0.00
October	29	F	15	11	73.33
October	30	J	18	0	0.00
November	31	J	18	0	0.00
November	32	J	15	0	0.00
November	33	M	17	10	58.82
November	34	M	20	13	65.00
November	35	F	16	13	81.25
November	36	M	18	11	61.11

Appendix 10

Infectivity of mice from North Prudence to larval ticks with *Borrelia burgdorferi*, 1987.

Month	Mouse No.	Sex	No. of Derived Nymphs	No. of Infected Nymphs	% Infectivity
May	1	M	16	14	87.50
May	2	M	15	15	100.00
May	3	F	14	11	78.57
May	4	F	20	16	80.00
May	5	M	20	18	90.00
June	6	M	16	16	100.00
June	7	F	15	12	80.00
June	8	M	19	6	31,58
July	9	F	15	14	93.33
July	10	F	13	12	92.31
July	11	M	19	7	36.84
July	12	M	17	9	52.94
August	13	J	18	15	83.33
September	14	J	15	0	0.00
September	15	J	19	2	10.53
September	16	F	20	13	65.00
October	17	J	15	0	0.00
October	18	J	17	0	0.00
October	19	J	19	0	0.00
October	20	M	20	14	70.00
October	21	F	16	11	68.75
November	22	M	20	12	60.00
November	23	M	18	11	61.11
November	24	F	20	0	0.00
November	25	M	15	9	60.00
November	26	J	15	0	0.00
November	27	J	20	0	0.00

Appendix 11

Analysis of variance for the three sites

South Prudence

Source	DF	Sum of Squares	Mean Squares	F Value	P
Model	6	4.532	0.755	5.988	0.0004
Error	28	3.532	1.260		
Corrected Total	34	8.064			

Prudence Park

Source	DF	Sum of Squares	Mean Squares	F Value	P
Model	6	2.858	0.476	3.641	0.0081
Error	29	3.794	0.131		
Corrected Total	35	6.651			

North Prudence

Source	DF	Sum of Squares	Mean Squares	F Value	P
Model	6	3.231	0.538	3.327	0.0194
Error	20	3.236	0.162		
Corrected Total	26	6.467			

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